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The Effect of Time and Stress on the Heart Rate-Oxygen Consumption Relationship of Uinta Ground Squirrels

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THE EFFECT OF TIME AND STRESS ON THE HEART RATE-OXYGEN CONSUMPTION RELATIONSHIP OF UINTA GROUND SQUIRRELS

by

Thomas E. Oldfield

A disseration submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Biology

Approved:

UTAH STATE UNIVERSITY
Logan, Utah

1975

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Thomas E. Oldfield

TABLE OF CONTENTS

Page

LIST OF TABLES

Table Page

LIST OF FIGURES

LIST OF FIGURES (Continued)

Figure Page

LIST OF FIGURES (Continued)

Figure Page

ABSTRACT

The Effect of Time and Stress on the Heart Rate-Oxygen Consumption Relationship of Uinta Ground Squirrels

by

Thomas E. Oldfield, Doctor of Philosophy

Utah State University, 1975

Major Professor: Dr. James A. Gessaman
Department: Biology

Uinta ground squirrels (Spermophilus armatus) were instrumented with ECG radio-transmitters. Heart rate and oxygen consumption were monitored for one hour at ambient temperatures above, within and below the thermoneutral zone. These measures were made at predetermined intervals throughout the active season of squirrels to determine if the heart rate-oxygen consumption relationship was a stable linear regression within and between squirrels during this period. Heart rate and oxygen consumption were also monitored for squirrels exposed to artificial and natural stressors. These squirrels were then released in an outdoor enclosure. Heart rate and behavior of animals were monitored simultaneously during above and below ground activity.

Heart rate-oxygen consumption regressions were stable during measurements through a 25°C temperature range. Regressions of heart rate versus oxygen consumption did vary between and within squirrels over four days.

Heart rate tended to decrease initially after presentation of natural stressors. Heart rate tended to increase when artificial stressors were presented. Regressions of heart rate versus oxygen consumption for these stressors tended to be linear, but heart rate would not be a good predictor of oxygen consumption during rapid heart rate changes because, in most cases, heart rate-oxygen consumption regressions were not statistically significant.

In some tests with rapidly decreasing initial heart rates, the heart rate-oxygen consumption relationship was negative. That is, oxygen consumption remained constant as heart rate decreased. Possible causes of negative responses are discussed.

Heart rate responses generated in laboratory stress tests were similar to semi free-living heart rate responses. During the major portion of time spent above and below ground, heart rate of squirrels was found to be quite stable. During these periods, heart rate should be a reasonable predictor of oxygen consumption.

In summary, average heart rate should be a reasonable predictor of oxygen consumption of free-living squirrels over daily periods. In using this method, it would be necessary to calculate regressions of heart rate and oxygen consumption in the laboratory before and after free-living studies to examine the stability of the regression lines during this period. An average regression line could be used to compensate in part for a change of the heart rate-oxygen consumption relationship during study periods.

(101 pages)

INTRODUCTION

Energy flow is an integral component of ecosystem analyses. One basic component of energy flow determination in an ecosystem is energy flow through animal populations. The magnitude of the energy requirements of a population is necessarily related to the energetic cost of maintenance of its members and the energetic cost of reproduction and growth. In an attempt to obtain reliable estimates of energy utilization for individuals of a population, investigators have estimated energy utilization of free-living animals by indirect and direct methods. Methods which derive estimates of free-living energetics through respirometric measurements made in the laboratory are defined in this paper as indirect. Methods which monitor free-living or semi free-living animals are defined as direct estimates of energy utilization.

The four common respirometric measurements utilized in estimating energy expenditure are: basal metabolic rate (BMR), fasting metabolic rate (FMR), resting metabolic rate (RMR), and average daily metabolic rate (ADMR) (Gessaman, 1973). Basal metabolic rate is a measure of energy expended by an animal in the post-absorptive state, at rest and at an air temperature which requires no additional energy for thermoregulation (thermoneutral zone). Fasting metabolic rate measures the energy expended by an animal in the post-absorptive state, in the thermoneutral zone and with some activity. Resting metabolic rate is a measure of energy expended by an animal which is not post-absorptive, but at rest at air temperatures below the thermoneutral zone (thermoregulating to maintain a constant body temperature), the BMR, FMR, and

RMR respiratory measurements are determined over periods of from one to three hours. The average daily metabolic rate determinations are conducted for 24 hour periods under conditions more closely approximating the natural environment of the animal. The four respirometric methods mentioned above estimate energy expenditures of animals in the laboratory by measuring oxygen consumption or carbon dioxide production.

Oxygen consumption is converted to Kcal (1 l of oxygen = 4.8 Kcal, assuming protein metabolism) to give an estimate of energy expenditure. Energy values obtained by the indirect methods are then corrected for the additional energy cost of free-living existence by multiplying them by 2 or 3 or by adding activity and/or growth components to them. The inadequacy of this approach is that an evaluation of the accuracy of the indirect approach requires actual measurements of free-living energy metabolism.

The only study comparing indirect and direct energy estimates is reported by Mullen and Chew (1973) in which they compared indirect (RMR) and direct (D_2O^{18} method) estimates of energy expenditure of free-living long-tailed pocket mice (Perognathus formosus). They found that the estimates by both methods were essentially the same. Mullen and Chew state that "this agreement was not unexpected, since the two methods show a large common component, i.e., the energy expended for thermoregulation." Another factor which probably contributed to the close agreement was the similarity between laboratory and free-living behavior of the long-tailed pocket mouse. Behavioral similarity may not be the case in other species. Mullen and Chew (1973) conclude "... thus, if prior knowledge is lacking concerning the metabolic behavior of a species in its natural environment, any indirect method of estimating that behavior would have to be validated by a direct method." Therefore, even though on indirect method has been shown to be a good estimator of free-living energy expenditure for Perognathus formosus, it is not known whether the same or other indirect methods are as good an estimate of free-living energy metabolism for other species.

Several direct methods of measuring free-living energy utilization have been proposed (e.g., monitoring radioisotope elimination rates, respiratory rate, D_2O and $H_2{}^{18}O$ turnover rates, and heart rate). The radioisotope method is based on the hypothesis that if an isotope has an excretion rate that is related to metabolic rate, then energy expenditure of a free-living animal could be determined by periodic measurements of the isotope level of the animal. Limited studies with iodine, zinc, calcium, strontium, cesium and phosphorus excretion rates have shown little promise for estimating free-living metabolism (Sawby, 1973).

The use of respiration rate to predict oxygen consumption has shown little promise for predicting free-living energy expenditure. In general, the respiratory rate of a bird or mammal under heat stress is not correlated with energy metabolism and at air temperatures below heat stress conditions, respiratory rate is correlated with energy metabolism only in animals that increase their respiratory rate and oxygen consumption inversely with air temperature (Hargrove and Gessaman, 1973).

The D_2O^{18} (heavy water) method of estimating free-living metabolism is based on the postulate that turnover rates of deuterium and ^{18}O injected into an animal are a measure of CO_2 production. Assuming oxygen is lost as CO_2 and H_2O and hydrogen is lost as H_2O, the difference between the turnover rate of ^{18}O and deuterium will represent the CO_2 loss (production). This method has been found to be in close agreement with values obtained with Haldane CO_2 determinations. Major drawbacks of this method are the cost of the isotopes and the analysis of the samples, the time necessary to conduct the analysis and the need to retrap the individuals (Mullen, 1971).

The heart rate-metabolic rate relationship is inferred by the relationship of heart rate and metabolic rate to air temperature, body temperature, and body weight (Johnson and Gessaman, 1973). The heart rate-metabolic rate relationship is linear for man, mammals and birds at rest, and for man and some mammals during strenuous (sub-maximal) exercise. This linear relationship is known to vary among individuals. It is not known conclusively whether the heart rate-metabolic rate relationship of mammals is linear during short term intraspecific or interspecific confrontations in the field or if the relationship for an individual changes over the course of a season.

The purpose of this study was twofold: 1) To examine the stability of the heart rate-metabolic rate relationship of individuals of a species over the period of one season and 2) To determine the heart rate-metabolic rate relationship of individuals of a species when exposed to various artificial and natural stressors in the laboratory and to determine whether the heart rate response of semi free-living individuals is similar.

REVIEW OF LITERATURE

Heart rate as a predictor of energy expenditure

Heart rate has been used as a predictor of energy expenditure in humans for many years (Johnson and Gessaman, 1973). Humans at rest have a positive linear relationship between heart rate and metabolic rate (Boas, 1932; Bevegard and Shepherd, 1967; Bradfield, Huntzicker and Fruehan, 1969) and during submaximal and maximal work (Booyens and Harvey, 1960; Chapman, Fisher and Sproule, 1960; Astrand et al., 1964; Andrews, 1967; Astrand and Rodahl, 1970; Cole and Miller, 1973). Although the heart rate-metabolic rate relationship has been shown to be a linear relationship and, therefore, a useful tool for predicting energy expenditures, there are several factors which limit and/or complicate the implementation of this relationship as a predictor of energy expenditures as applied to groups of individuals. Berggren and Christensen (1950), Booyens and Harvey (1960), Andrews (1967), Bradfield, Huntzicker and Fruehan (1969), Datta and Ramanthan (1969), Bradfield (1971), and Cole and Miller (1973) have observed that the equation describing the linearity of the heart rate-metabolic rate relationship changes with the type of work performed by an individual and is different among individuals. Bradfield, Huntzicker and Fruehan (1969) also noted the heart rate-metabolic rate linear relationship varied with each individual and between days of the tests for the same individual. Boas (1932), Booyens and Harvey (1960) and Datta and Ramanthan (1969) commented on the need to conduct tests under controlled conditions to eliminate, as much as possible, the environmental and psychological conditions which affect the heart rate-metabolic rate relationship.

One possible method for reducing the variability observed in the heart rate-metabolic rate relationship is to average heart rate over the entire test period rather than determine average heart rate for each activity (Bradfield, Huntzicker and Fruehan, 1969). This may partially correct the problem in studies intended to estimate energy expenditures of individuals over daily or weekly time periods, but for studies of shorter duration this may not be applicable. Another approach to the problem is determination of the relationship of net heart rate to metabolic rate. Andrews (1971) calculated net heart rate from the following equation:

$$NHR = GHR - RHR$$

where

NHR is net heart rate for the activity

GHR is the gross measure of heart rate for the experimental run

RHR is the mean heart rate for the subject during relaxed standing trials

Andrews reported that through the calculation of net heart rate the subject to subject variation in the regression equation was reduced to statistical insignificance and by lumping activity patterns of all subjects into 15 categories, each of which had activities with similar circulatory patterns, the error due to different activities was reduced.

Laboratory studies of heart rate have been conducted on dogs (Barger et al., 1956; Bailie et al., 1961), cattle (Blaxter and Wood, 1951 and Bianca, 1958) and sheep (Blaxter and Wood, 1951) with results similar to those observed in human studies. Two notable studies of penned sheep were reported in the late 1960's. Webster (1967) studied the heart rate-metabolic rate of nine wether sheep (Webster reported the measurements of only four sheep, however, Brockway and McEwan (1969) learned through personal communication that in actuality nine sheep had been used) using "hard wire" EKG leads and a ventilated hood for measuring oxygen consumption. The animals were held in standing or lying positions and measured when quiet. Webster was able to predict metabolism from the heart rate-metabolic rate with 6-13% of measured metabolic rates in four sheep while little or no correlation was observed in the remaining five sheep. Webster concluded that heart rate has an application in predicting heat production of free-living animals. Brockway and McEwan (1969) also investigated the heart rate-metabolic rate of sheep with "hard wire" heart rate leads and a ventilated hood. Heart rate and metabolic rate were not correlated in four ewes while they were weakly correlated in one wether sheep (20-25% prediction error). Brockway and McEwan concluded that the heart rate method of predicting energy expenditure is of limited value until it is proven that muscular activity and the emotional state of the animal have no negative effects on the heart rate-metabolic rate curves. In addition the use of "hard wire" leads in heart rate measurements may cause stress and physical restraints on the animals which could account for the poor correlations.

The development of smaller electrical components has alleviated the problem of constraint to a great degree through manufacture of ECG transmitters of sufficiently small size and weight to allow implantation of animals with small radio transmitters. These cause minimal stress and allow the animal total freedom of movement. Gilmer et al. (1974) observed no noticeable effects of radio packages on free-flying mallards and wood ducks. He reported the period of adaptation to be one day for most ducks and possibly a more subtle adjustment of a much longer time period. Tester (1971) observed an adaptation period of as long as one to two weeks in mammals and birds. Dumke and Pils (1973) reported pheasants adjusted to radio packages with one to two days. Ruff (1971) observed three Unita ground squirrels fitted with dummy EKG transmitters for two months and observed no adverse behavioral or physiological effects.

These smaller ECG transmitters have been used in several studies in the laboratory and in the field. Morhardt and Morhardt (1969) abdominally implanted ECG transmitters in Belding ground squirrels (Spermophilus beldingi beldingi) and monitored their heart rate-metabolic rate in metabolism chambers. Two squirrels were then released in outdoor cages and heart rate recorded during 24-hour periods. A single squirrel was released in the natural habitat and several hours of heart rate recorded. Heart rate was well correlated with 0_2 consumption at different temperatures and levels of activity in the laboratory. The heart rates of the caged and free-living animals were similar and higher than those observed in metabolism chambers. Owen (1969) reported a linear correlation between heart rate and metabolized energy of blue-winged teal in the laboratory. Teal, free to swim in an outdoor pond, but unable to fly, had heart rates consistently higher than heart rates under controlled conditions. The semi free-living birds exhibited feeding and swimming heart rates which were not statistically different from resting heart rates. Heart rate did increase 30% when preening and 60% when swimming rapidly. Ruff (1971) observed somewhat similar increases in Uinta ground squirrels (*S. armatus*) during feeding, grooming and burrow activity with increases of 19, 31 and 30 beats per minute respectively over inactive heart rate levels. Observations of heart rate in response to social interactions indicated that dominants usually exhibit less stress response than subordinates and the magnitude of the heart rate response is not as good an indicator of agonistic behavior as the maximum heart rate attained in response to a social interaction (Ruff, 1971).

A comparison of the heart rate-metabolism relationship for six small mammal species was reported by Morhardt and Morhardt (1971). The results of this study showed significant correlations (>0.9) between heart rate and metabolic rate for Belding's ground squirrel (*S. beldingi beldingi*), California ground squirrel (*S. beecheyi parvulus*), golden mantled ground squirrel (*S. lateralis chrysodeirus*), California mouse (*Peromyscus californicus insignis*), bushy-tailed woodrat (*Neotoma cineria acraia*), albino rat and golden hamster (*Mesocricetus auratus*) in the laboratory. The correlations were significantly linear in all animals except one albino rat, the golden hamster, and the California mice which had curvilinear relationships. The Morhardts' postulated these curvilinear relationships. The Morhardts' postulated these curvilinear relationships were due to the animals functioning at or near the maximum heart rate for the species. At the maximum heart rate, oxygen consumption will continue to increase as heart rate levels off with the $A\text{-}V_{O_2}$ difference increasing to compensate. They reasoned that the other animals were not at maximum heart rate which resulted in the linear correlation between heart rate and 0_2 consumption. The Morhardts' also observed a significant correlation between heart rate and oxygen consumption with changes in activity as well as temperature and that tapping on the cage produced a heart rate-metabolism relationship similar to that of lowering ambient temperature. The slopes of the regression lines for the heart rate-metabolism relationship varied between individuals of the same species and for the same individual over several days or months was not significantly different at the 95% level except at extremely high or low rate values. In a later study Johnson (1973) noted in two semi free-living Uinta ground squirrels (S. armatus) that the slopes of heart rate-metabolic rate regressions measured 5 days apart had changed significantly and that the standard deviations did not overlap at any point along the regression line. He also observed a significant linear correlation between heart rate and metabolism of Unita ground squirrels in the laboratory and the slope of the heart rate-metabolism regression varied between individuals.

A study of white-throated sparrows (Zonotrichia albicollis) by Fanning (1973) showed a direct correlation between heart rate and oxygen consumption. From this observation, she suggested that the use of heart rate might be a valuable approach in determining field metabolism.

To my knowledge, the most recent study of semi free-living and free-living heart rate of mammals has been conducted by Lund (1974) with black-tailed prairie dogs (Cynomys ludovicianus). In five prairie dogs, he found:

> ... the probability of obtaining a good linear relationship between heart rate and oxygen consumption equally high between and within animals from the observation that the variance of correlation coefficients of heart rate-metabolism regression lines among animals was not greater than within animals and, in fact, less.

He also reported that the association between heart rate and oxygen consumption was linear over rapid changes in variables, different levels of activity and time. The regression lines were different over several weeks to months, possibly due to seasonal trends or changes in body weights. A mathematical model was developed for determining time and energy expenditures over 24-hour periods.

Short term responses of heart rate to stress

The heart rate response to psychological factors is not as clear cut as heart rate response during rest or physical exercise. Lacey and Lacey (1958) observed that heart rate did not behave consistently between individuals. In cold tests (foot in ice water) on human subjects a significant number of subjects had increased heart rates, whereas in mental arithmetic and word fluency tests the heart rate decreased in a larger proportion of the subjects.

Heart rate has been observed to respond with either an increase or decrease in response to various stresses, i.e., noise, shock, light, conspecifics and predators. Boas (1932) reported heart rate in humans slowed with attention to visual and acoustic stimuli, fright, tension and sensual and intellectually pleasurable experiences, while heart rate increased with excitement and sensual and intellectually unpleasant experiences. Sokolov (1963) attributed the two major types of heart rate response to a system whose role is either to facilitate or inhibit sensory stimulation. He defined three types of response to environmental stimuli: 1) adaptive response which occurs only to a certain quality of stimulus (e.g. thermal stimulation) and may cause an increase or decrease in heart rate response; 2) defensive response which is not specific to quality of stimulus and is limited to intense stimuli (heart rate will increase in this response); 3) the orienting response which occurs for any change in stimulus conditions and functions to facilitate reception of sensory information (heart rate will decrease in this response). Lacey et al. (1963), Obrist (1963), Galin and Lacey (1973) and Duncan-Johnson and Coles (1974) made similar observations in which stimuli that evoke attention to the environment will induce cardiac deceleration while those evoking rejection of the environment will induce cardiac acceleration.

Several studies have reported results generally in agreement with the types of response outlined by Sokolov (1963). Chalmers and Levine (1974) observed heart rate acceleration in response to strong shock (2mA for 0.1 sec. duration) during the neural development of neonatal rats. Smith and Strawbridge (1969) observed increased heart rate and respiration rate in response to auditory stimuli and an increased respiration rate and decreased heart rate in response to light. Bond (1943) monitored the heart rate response of dogs and cats to noise and found an initial increase in heart rate with a decrease occurring 10 seconds later. This was followed by undulations of heart rate from two to seven minutes. Thompson et al. (1969) working with starlings found the initial increase of heart rate in response to sound was affected by the time of day and the absence or presence of conspecifics. Harris and Siegel (1967), Ruff (1971) and Cherkovich and Totoyan (1973) reported increased heart rates during social interactions with the magnitude of increase related to the relative dominance of the individuals. A study by Mancia, Baccelli and Zanchetti (1972) reported variable heart rate response in six cats when confronted with another cat, dog, mouse and fire. Two of six cats exhibited tachycardia when confronted with a mouse, four of six cats exhibited tachycardia when confronted with a dog, one cat exhibited no change, one bradycardia, and one tachycardia when confronted with fire. One of six cats exhibited bradycardia when confronted with another cat. The variability of heart rate response may have been due to the initial level of heart rate prior to the stimulus.

The magnitude of the heart rate response to stressors will vary depending on the prestimulus heart rate level. Wilder (1962) states that

> given a standard dose of stimulus and a standard period of measurement, the response, that is, the change from the initial value (prestimulus), will tend to be smaller when the (IV) initial value is higher, this applies to functioning raising stimuli."

For function-depressing stimuli negative correlations become positive. He also noted that beyond a certain range of IV's there is an increasing tendency sometimes for no response and frequently toward reversed responses. The higher these extreme IV's the more frequent are the reversals on function-raising stimuli and the lower the IV's the more frequent are the reversals of function-depressing stimuli. Hord, Johnson and Lubin (1964) related these responses to homeostasis. They hypothesized that the measured magnitude of an autonomic response is the result of neural and endocrine levels controlled by the relative amounts of sympathetic and parasympathetic innervation and by the momentary prestimulus level. Thus, high heart rate is accompanied by a relatively high level of tonic activity and when a stimulus initiates an increase in heart rate, the high level of tonic activity in the sympathetic and parasympathetic systems immediately checks the increase in heart rate causing a small increase or decrease. The same reasoning applies to low heart rates with a greater increase in heart rate occurring before the parasympathetic system checks the heart rate.

METHODS

General

Ten adult female Uinta ground squirrels (S. armatus) were live trapped at the Utah State University Forestry Camp on April 29, 1974 and brought into the laboratory to examine for pregnancy. Rugg (1971) reported Uinta ground squirrels breed in early April, one to several days after emergence from their hibernaculae. Non-pregnant females were used in this study to eliminate potential effects of parturition and lactation on the heart rate-metabolism relationship. Two of the ground squirrels were released in an outdoor pen for later semi free-living studies while eight individuals were retained in the laboratory for subsequent measurements of resting metabolic rate (RMR) and heart rate. Five additional females were trapped in June and three females in July for stress and semi free-living studies. In August, seven juvenile, female ground squirrels were live-trapped for further stress and semi free-living studies.

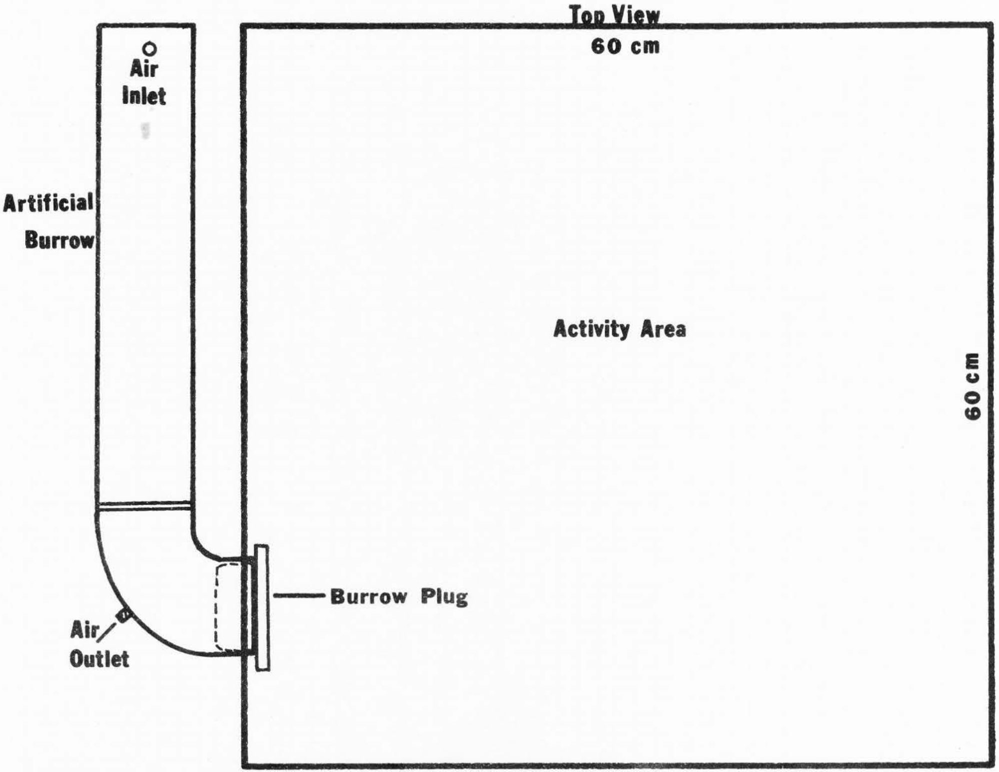
One to three days prior to an experiment an animal was fitted with a small FM ECG transmitter (Narco Bio-systems, Inc., Houston, Texas). The transmitter was attached to a nylon collar that could be easily fitted around the squirrel's neck. Two small O-ring type silver electrodes were connected to the transmitter by fine, teflon coated, stainless steel lead wires. The completed transmitter collar weighed approximately 9 grams with batteries. The squirrel was deeply anesthetized with ether; and an incision ran laterally from the midventral line.

Both electrodes were inserted subcutaneously through this incision. One was sutured into place on the opposite side of the neck and the other was positioned ventrally over the mid-sternal region. The incision was sutured tightly closed and the collar snugly fitted into place.

Animals used in semi free-living studies were released the day following transmitter attachment to allow for maximal recording time (the transmitter battery life was 5 to 6 days). Resting metabolic rate and stress experiments were conducted three days after electrode implantation to allow for a more complete recovery from surgery and ether anesthesia. The implantation and collared transmitter did not affect the overt behavior of the squirrels.

Resting metabolic rate-heart rate measurements

Resting metabolic rates (RMR) were measured on eight ground squirrels in a sheet metal box (60 cm X 60 cm X 30 cm) with a transparent plexiglass top, subsequently referred to as a metabolism chamber (Figure 1). The box was housed in a walk-in environmental chamber with temperature and photoperiod controls. An animal was placed in the metabolism chamber the day following attachment of the heart rate transmitter and was allowed two days to become familiar with the chamber. An artificial burrow constructed of 7.5 cm I.D. black PVC irrigation pipe was attached to one side of the box. The artificial burrow consisted of a PVC elbow fastened to the sheet metal chamber and jointed to a 45 cm length of straight pipe sealed at the distal end. Plastic tube connectors were threaded into the elbow and into the sealed end to provide an air inlet and outlet. All RMR measurements were made after 19:00 hours when human


Top View
60 cm
Air Inlet
Artificial Burrow
Activity Area
60 cm
Burrow Plug
Air Outlet

activity in the laboratory was minimal. Prior to an RMR measurement the open end of the artificial burrow was sealed with a rubber gasket (the type used to plug irrigation pipe) about 30 minutes after the animal had entered the burrow for the night. At the time the burrow was sealed a dynapump was turned on and dried room air was continuously pumped through the artificial burrow at approximately one liter/minute (STP). The rate of air flow to the metabolism chamber was controlled and monitored by Matheson Model 603 flowmeters (The Matheson Co., Inc., E. Rutherford, N. J.). The flowmeters were calibrated immediately before and after each one-hour measurement by a Vol-U-Meter (Brooks Instrument Div., Emerson Electric Co., Hatfield, Penn., Model 1057) flowmeter. A one-hour equibration time preceded RMR measurements at each temperature. Heart rate and 0_2 consumption were then measured for one hour at each temperature. ECG signals were received by a FM receiver (Narco Bio-systems, Inc., Houston, Texas) and recorded on a physiograph (Model IV, Narco Bio-systems, Inc., Houston, Texas). Heart rate was determined by counting the R waves for a five-second interval of every minute of recording. The five-second recordings were then converted to beats per minute and averaged for the one-hour measurements. Oxygen consumption was monitored with a Beckman G-2 paramagnetic oxygen analyzer. Oxygen consumption was computed using the equation for open-flow systems of Depocas and Hart (1957) and was averaged over the one-hour measurements. The oxygen analyzer was equipped with an automatic 5-channel selector so that one to five animals could be monitored during the one-hour periods. The channel selector monitored each channel being used for five minutes. This sequence was interrupted for 2.5 minutes every 30 minutes when room air was automatically drawn into the analyzer to rezero its calibration. In the RMR experiments, three animals were monitored during the same hour, i.e., the 0_2 consumption of each animal was measured for approximately three, five-minute periods during the hour. An average of these values was computed for each hour.

Stress experiments

The stress experiments were conducted on 17 ground squirrels in a manner similar to RMR experiments. The animals were fitted with a heart rate transmitter three days prior to an experiment. Each animal was placed in a small metabolism chamber four to five hours preceding the introduction of the stimulus to allow the animal time to calm down after handling. A dynaflow pump was turned on to create white noise and to supply 4 liters/minute (STP) of dried air to the chamber for the duration of the experiment. The metabolism chamber for the stress experiments had a volume of 3.6 liters (minus the volume of the animal). Three sides and the bottom were constructed of 0.635 cm plywood. One side and removable top were made of 1.47 cm transparent plexiglass. A metal shock grid was mounted in the bottom of the chamber. A Grass SD9 Stimulator (Grass Medical Instruments, Quincy, Mass.) was used to deliver an electrical stimulus to the grid (Figure 2). The chamber was sealed with fiberglass resin to prevent air leakage. This metabolism chamber was located inside a larger plywood box lined with 1 inch styrofoam on all walls and the bottom to reduce outside noise and shield the experimenter from the animals view during experimentation. Four different stimuli

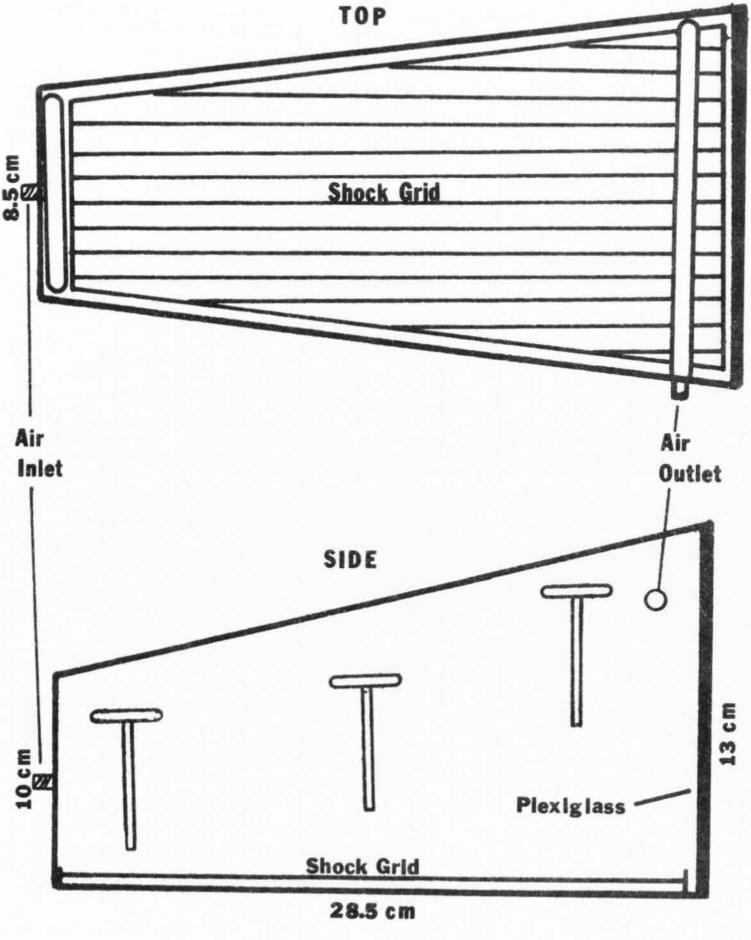


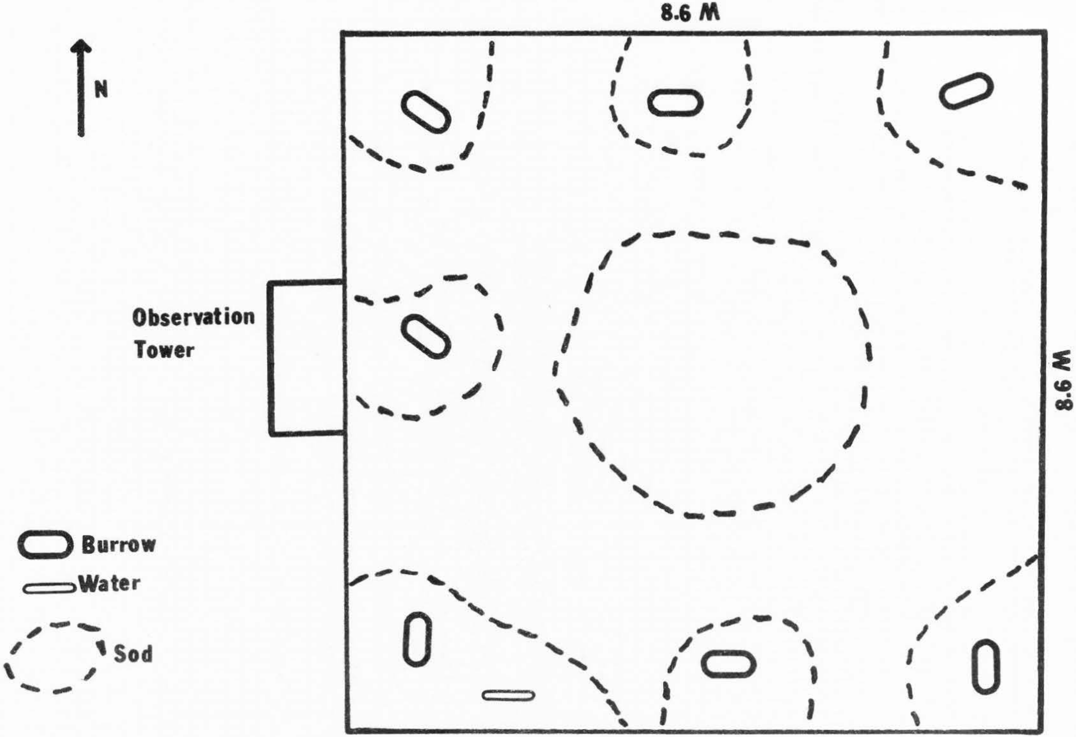
Figure 2. Schematic diagram of the metabolism chamber used in determination of heart rate and oxygen consumption responses of seventeen Uinta ground squirrels to various natural and artificial stressors.

were placed in the box through an opening in one wall of the larger box which shielded the experimenter from the animal. These included a mounted badger, a mounted great horned owl, a cardboard silhouette of a hawk and conspecifics. Noise and shock were also used as stimuli. Squirrels were subjected to noise made by hitting a garbage can cover with a hammer for 10 seconds. Animals were shocked with a square wave stimulus of 1 to 2 mA for a ten second period. Confinement was accomplished by holding an animal and monitoring its 0_2 consumption by means of a mask placed over its head. The stimuli were presented to the experimental animal in a random order with 45 minutes to one hour intervals between presentation of each stressor. Each stimulus was presented to the animal for 10 to 30 seconds. Heart rate and 0_2 consumption were monitored for 10 to 15 minutes following the stimulus or until the heart rate and 0_2 consumption returned to pre-stimulus values. Electrocardiograms were monitored continuously during the experiment by the methods described previously and the heart rate was averaged over five-second intervals. Oxygen consumption (ml/g/min) was measured continuously with a Beckman OM-11 oxygen analyzer.

An inherent problem in using metabolism chambers to measure oxygen consumption is a lag between the time an animal consumes a percentage of oxygen from incoming air and the registering of this percent change on the analyzer. This lag time is a result of mixing of air in the metabolism chamber. To minimize lag time, a small volume metabolism chamber and a fast flow rate of incoming air were used in this study. To determine the lag time for the system, a volume of gas of known oxygen percent (standard gas) was flushed through the chamber, and the time delay between injection of the standard gas and recording of that oxygen change on the analyzer was noted. The time delay between presentation of stimulus and recording of a change in oxygen percent of outflowing air was also noted in all stress experiments, except confinement. In confinement experiments, no time delay was noted because a mask was used to collect expired air and the volume of air in the mask was negligible with respect to mixing. The average time lag in recording percent oxygen changes in outflowing air for the standard gas measurements and from actual stress tests was 8 seconds. A correction for this 8 second delay in the response of the analyzer was made when heart rate and oxygen consumption changes were compared with stimulus presentation.

Semi free-living experiments

Behavior and heart rate were monitored on 10 semi free-living animals in an outdoor enclosure 8.69 X 8.69 meters (Figure 3). The enclosure was surrounded by white sheet metal walls, 2.4 meters high. Chicken wire lay 10 cm beneath the dirt floor and covered the top of the enclosure. Seven artificial burrows constructed of 7.6 cm diameter heavy cardboard tubing were placed on the floor of the enclosure and covered with 25 cm of dirt. Sod was placed over and around burrows and covered about one-half of the floor area. Sagebrush was placed in the enclosure for cover and shade. Animals were given food and water *ad lib*. Behavior and heart rate were monitored from an observation tower located on the west wall of the enclosure. Heart rate was monitored with the same instrumentation used in RMR and stress experiments. An FM antenna was hung in the enclosure to provide better pick-up of ECG signals. Heart rate was averaged over five-second intervals and converted to beats per


N
8.6 M
Observation
Tower
8.6 M
Burrow
Water
Sod

minute for each behavior observed. Behaviors monitored were grooming, feeding, drinking, digging, sunning, stationary on all 4 legs, alert (upright on hind legs) and social interactions with conspecifics.

Animals were released in the enclosure two weeks prior to attachment of the transmitter. Thirty-six hours before the monitoring of an individual, the animal was live-trapped in the evening, brought into the laboratory for attachment of the transmitter and returned to the enclosure the next morning. The animals were monitored only in the morning and evenings because little, if any, above ground activity occurred during the afternoon. After these observations the animals were again live-trapped and brought to the laboratory for replacement of ECG transmitter batteries and for stress and RMR experiments.

RESULTS

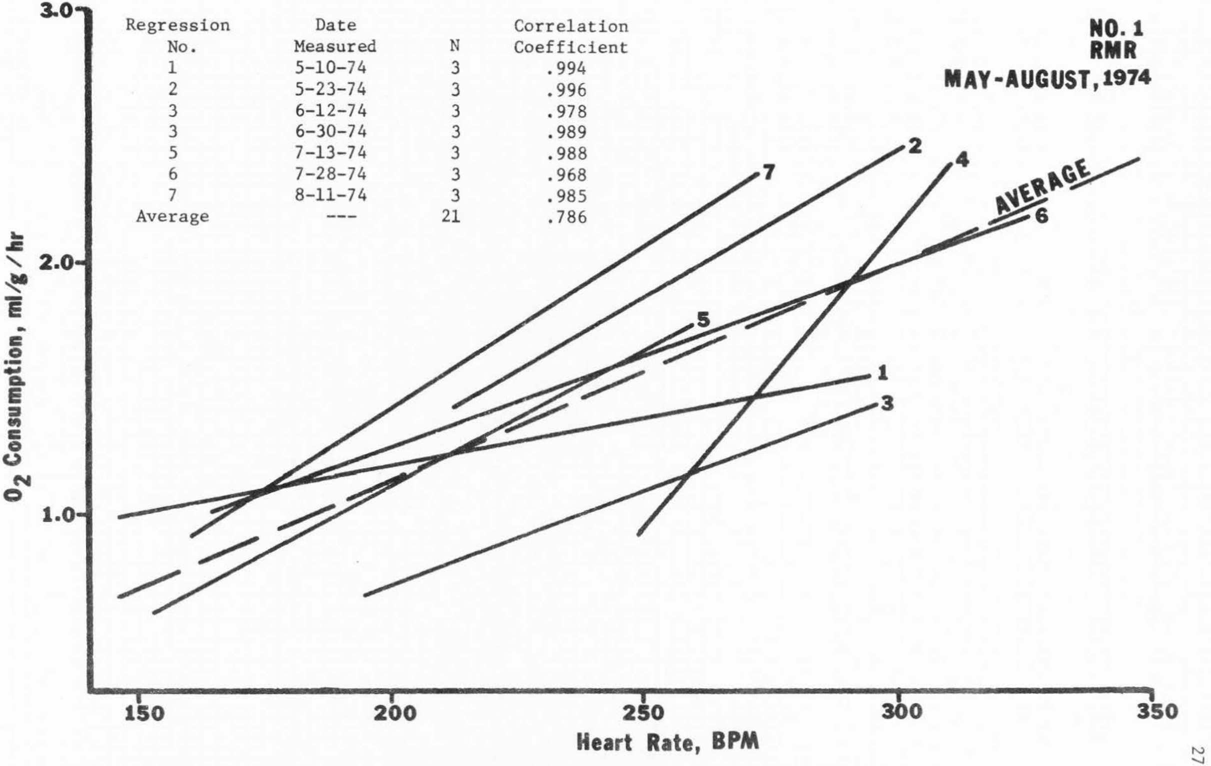
Resting metabolic rate-heart rate measurements

Resting metabolic rate-heart rate regressions were measured for eight Uinta ground squirrels on several different days between May and September, 1974, to determine the stability of the heart rate-oxygen consumption linear relationship for individuals during the non-hibernating season. Three non-pregnant females were monitored approximately every two weeks from May to July. In July all three animals developed a severe infection around the incision where heart rate electrodes were implanted. All measurements on these females were terminated at this time. Three females which had been pregnant at time of capture were not monitored until the young were weaned in early June. These animals were monitored approximately every two weeks from June through August. In mid-August the animals began to have bouts of torpor and were no longer monitored. I assumed these animals were changing physiologically in preparation for entry into hibernation. Three other non-pregnant females were trapped in late June and monitored from July through early September when they began to have bouts of torpor. Resting metabolic rate-heart rate regressions were also calculated over a five-day period for two animals in September.

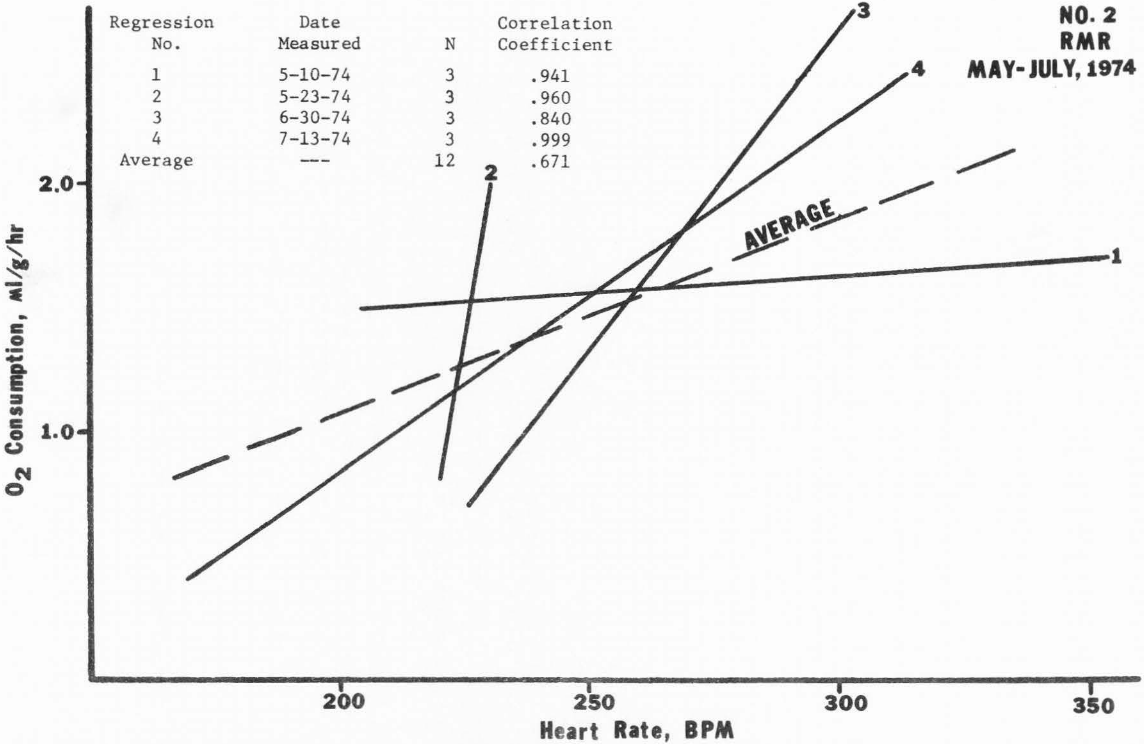
Forty-nine heart rate-oxygen consumption regressions were calculated during the study period. Ten of the heart rate-oxygen consumption relationships were determined only once for animals subsequently monitored in stress experiments and during semi free-living conditions. Three of these regressions had an insufficient number of values and were not considered in later calculations. A positive linear relationship between heart rate and oxygen consumption was observed in the remaining forty-six measures. Forty-two of the forty-six positive heart rate-oxygen consumption relationships had correlation coefficients of 0.90 or greater which is statistically significant at 0.05. The remaining four relationships had correlation coefficients of 0.80 to 0.89 which were not statistically significant at 0.05.

The heart rate-oxygen consumption regressions measured at different times during the non-hibernating season were compared for each animal (Figures 4-11). In seven of eight animals, the one-tailed F test showed no significant difference between slopes at 0.05. In six of eight animals, the one-tailed F test showed no significant difference between elevations at 0.05. Although there was no statistical significance between regression lines of individual animals over the non-hibernating season, there was statistical significance between regression lines calculated over periods within the non-hibernating season. The statistical insignificance for the entire non-hibernating season was due to the wide scatter of individual values used to calculate the regression lines.

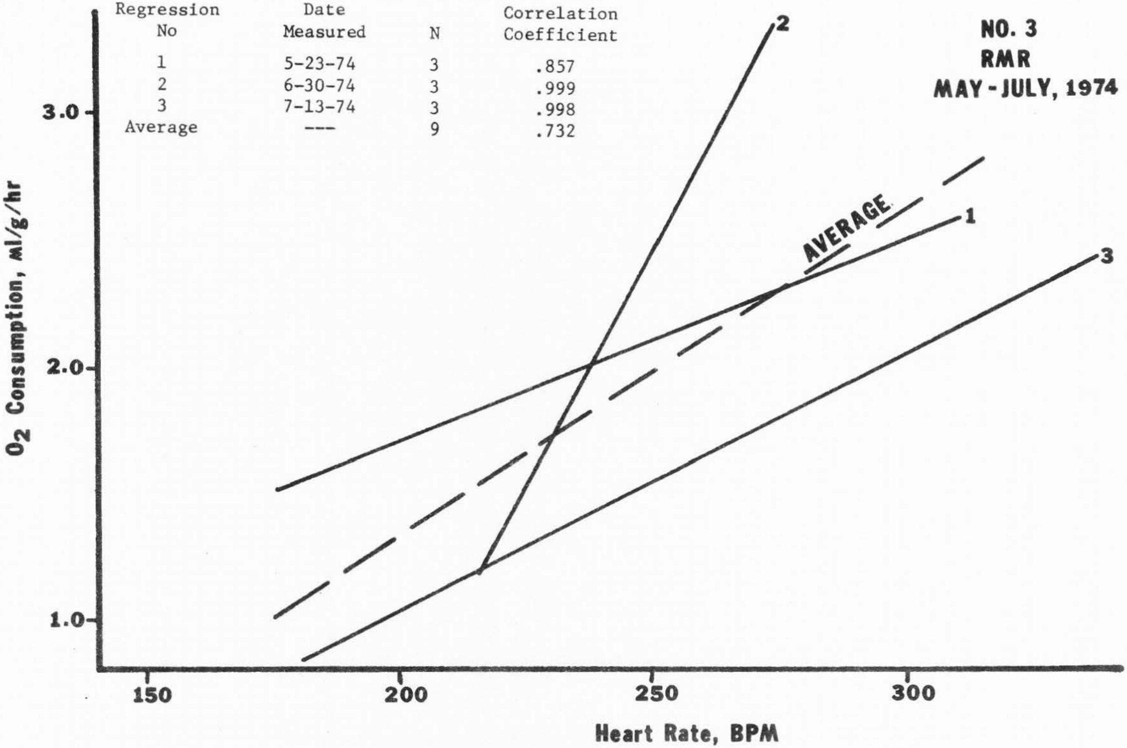
Figure 12 shows average regression lines calculated for each individual animal monitored during the active season from the equation $\hat{y} = \bar{y} + b\ (x-\bar{x})$ (Snedecor and Cochran, 1971). The slope (b) calculated from pooled regression lines of each individual were used in this equation. Comparison of these average regression lines with the one-tailed F test showed no significant difference between the slopes and elevations



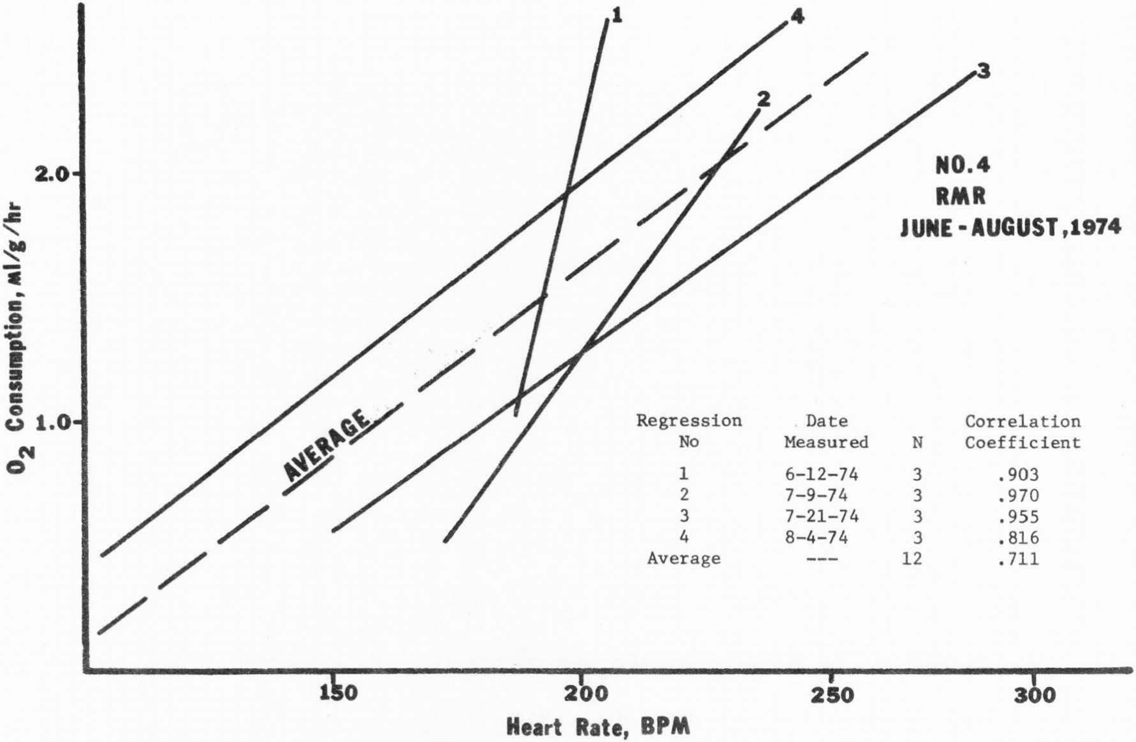
Regression No.	Date Measured	N	Correlation Coefficient
1	5-10-74	3	.994
2	5-23-74	3	.996
3	6-12-74	3	.978
3	6-30-74	3	.989
5	7-13-74	3	.988
6	7-28-74	3	.968
7	8-11-74	3	.985
Average	---	21	.786



Regression No.	Date Measured	N	Correlation Coefficient
1	5-10-74	3	.941
2	5-23-74	3	.960
3	6-30-74	3	.840
4	7-13-74	3	.999
Average	---	12	.671

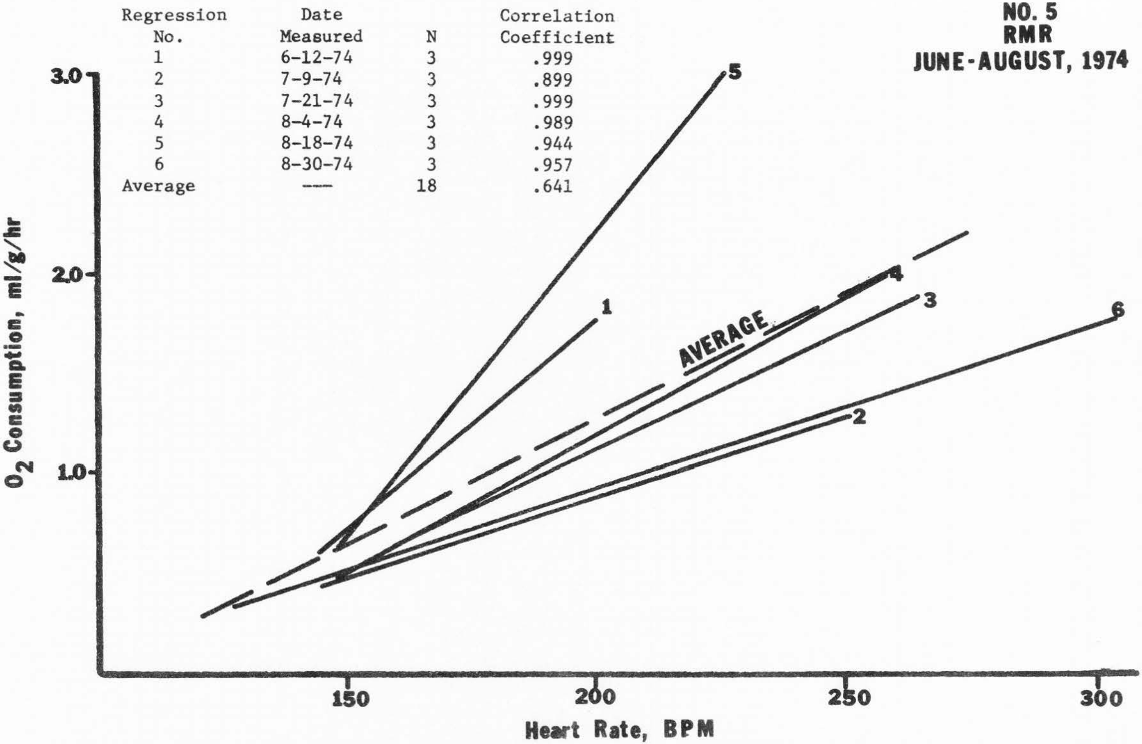


Regression No	Date Measured	N	Correlation Coefficient
1	5-23-74	3	.857
2	6-30-74	3	.999
3	7-13-74	3	.998
Average	---	9	.732



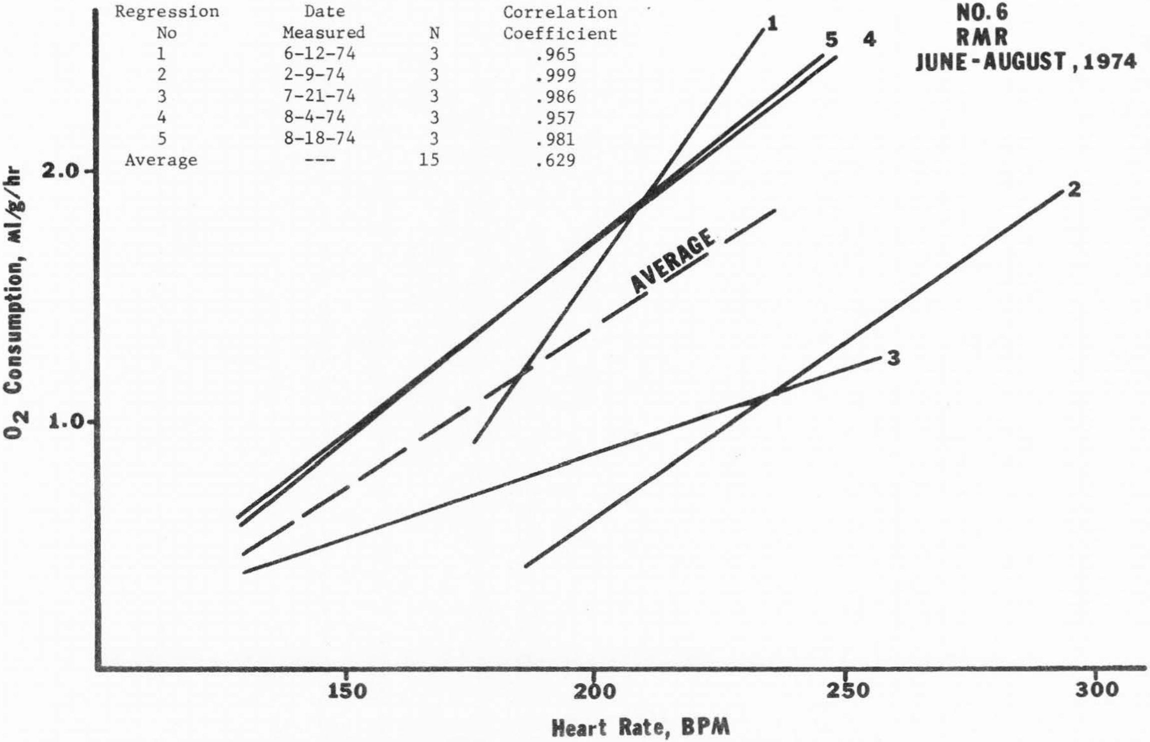
NO.4
RMR
JUNE - AUGUST,1974

Regression No	Date Measured	N	Correlation Coefficient
1	6-12-74	3	.903
2	7-9-74	3	.970
3	7-21-74	3	.955
4	8-4-74	3	.816
Average	---	12	.711

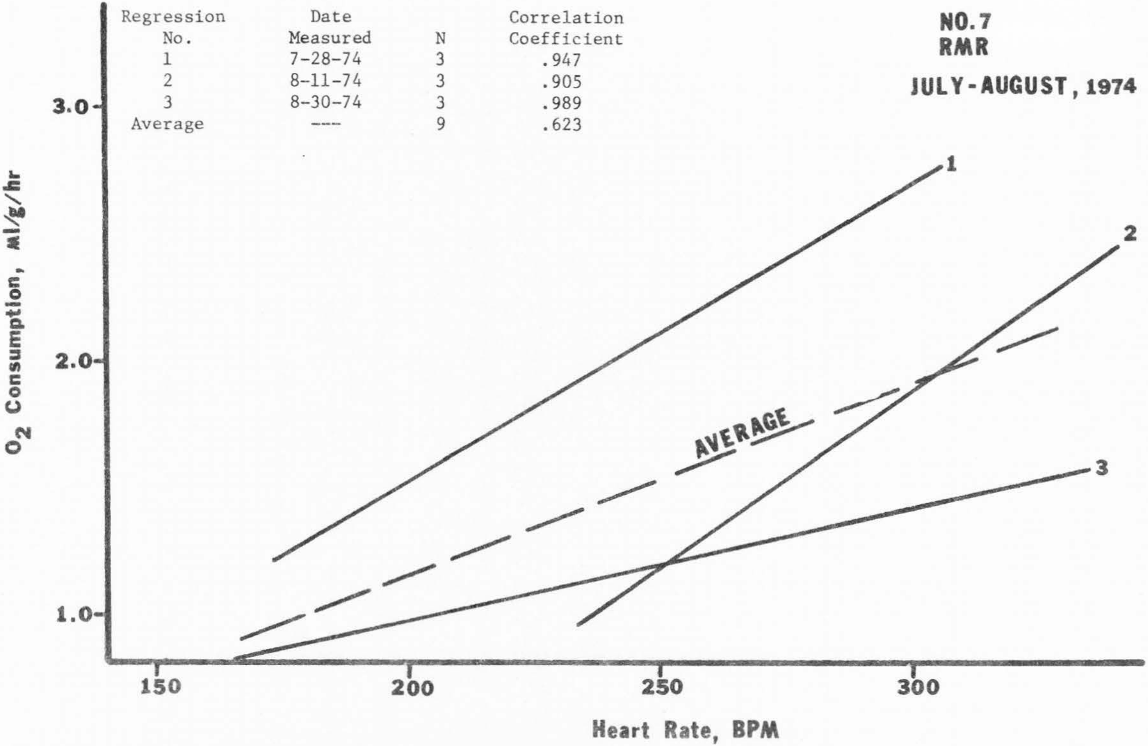


NO. 5
RMR
JUNE-AUGUST, 1974

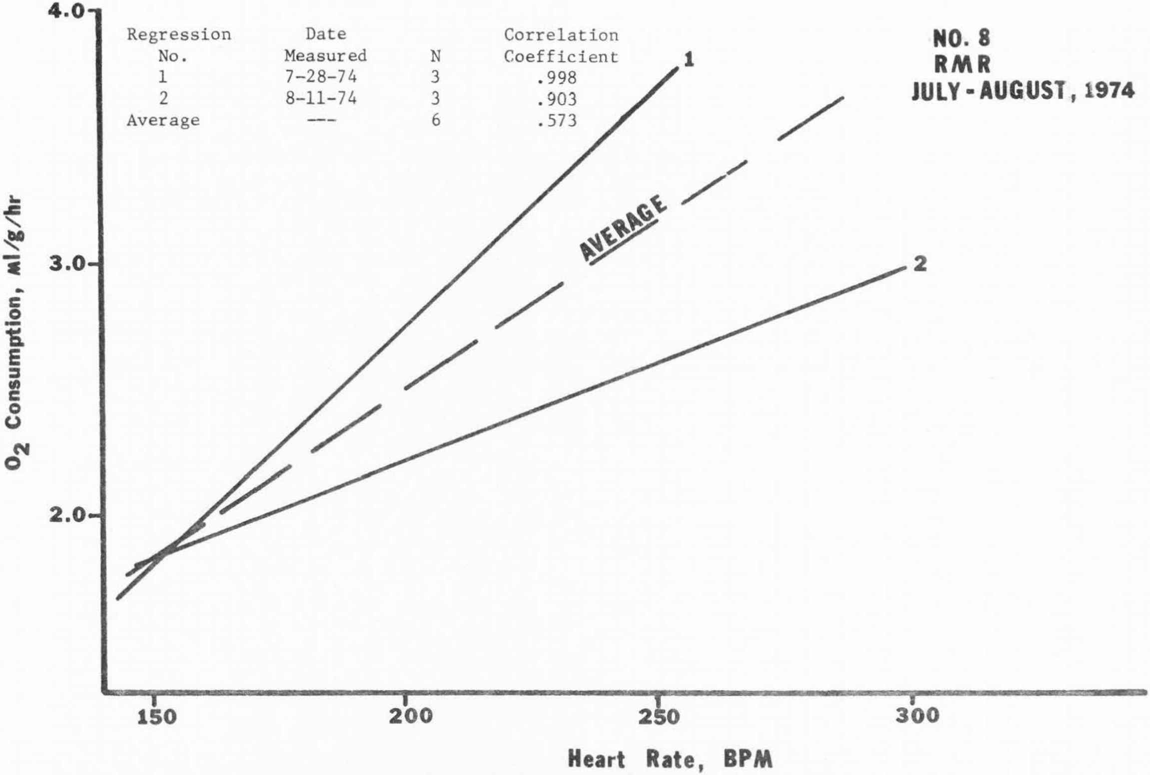
Regression No.	Date Measured	N	Correlation Coefficient
1	6-12-74	3	.999
2	7-9-74	3	.899
3	7-21-74	3	.999
4	8-4-74	3	.989
5	8-18-74	3	.944
6	8-30-74	3	.957
Average	---	18	.641



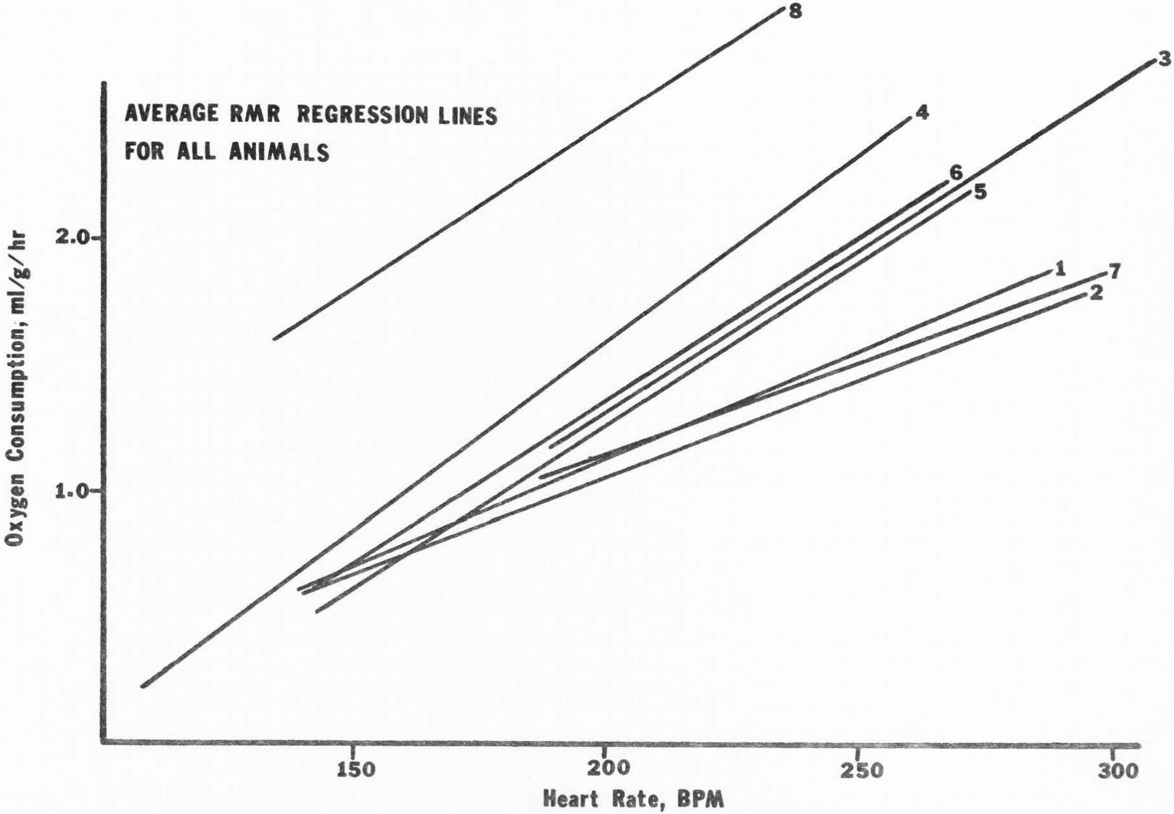
Regression No	Date Measured	N	Correlation Coefficient
1	6-12-74	3	.965
2	2-9-74	3	.999
3	7-21-74	3	.986
4	8-4-74	3	.957
5	8-18-74	3	.981
Average	---	15	.629



Regression No.	Date Measured	N	Correlation Coefficient
1	7-28-74	3	.947
2	8-11-74	3	.905
3	8-30-74	3	.989
Average	----	9	.623



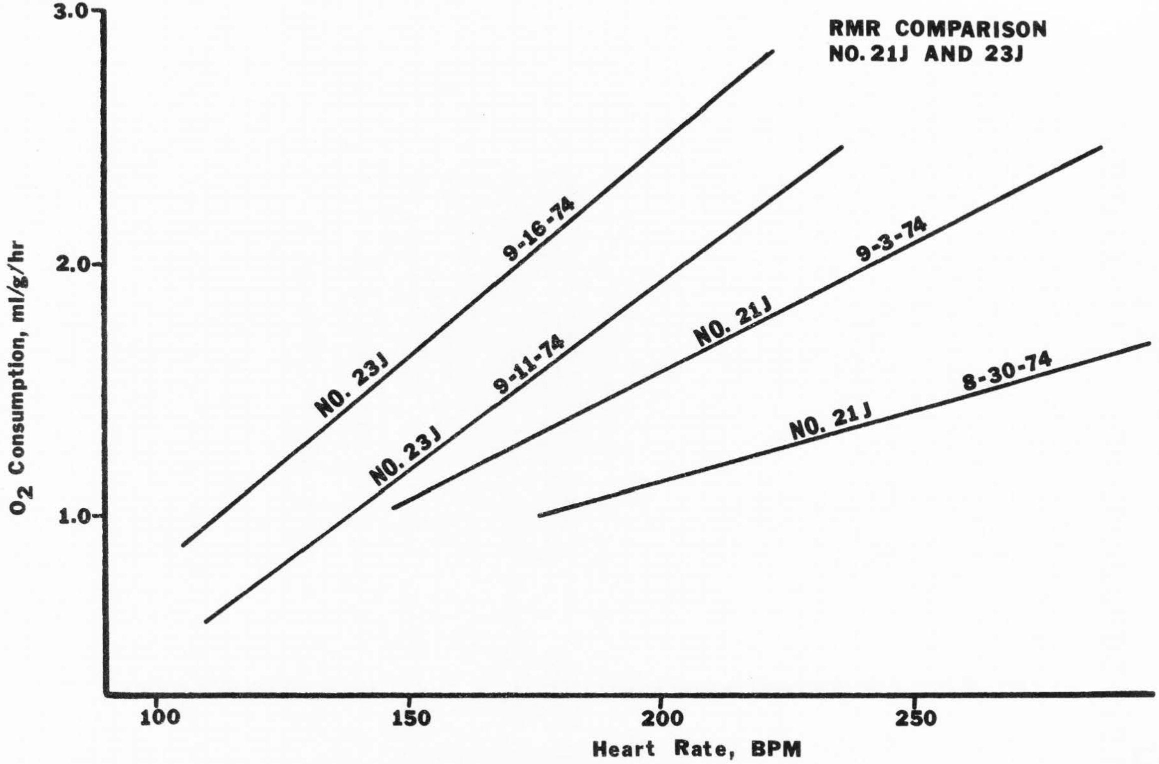
Regression No.	Date Measured	N	Correlation Coefficient
1	7-28-74	3	.998
2	8-11-74	3	.903
Average	---	6	.573


AVERAGE RMR REGRESSION LINES
FOR ALL ANIMALS
Oxygen Consumption, ml/g/hr
2.0
1.0
150
200
250
300
Heart Rate, BPM
8
3
4
6
5
1
7
2

of these lines at 0.05. The average regression line of animal number 8 was not included in these calculations because it had developed an infection at the site of the implant incision after the first measurement and subsequent heart rate and oxygen consumption values were consistently higher than in other individuals. Comparison of regression lines of the heart rate-oxygen consumption relationship of each of two individuals monitored for five days indicated no statistically significant difference between the slopes of the regression lines for each individual at 0.05 (Figure 13).

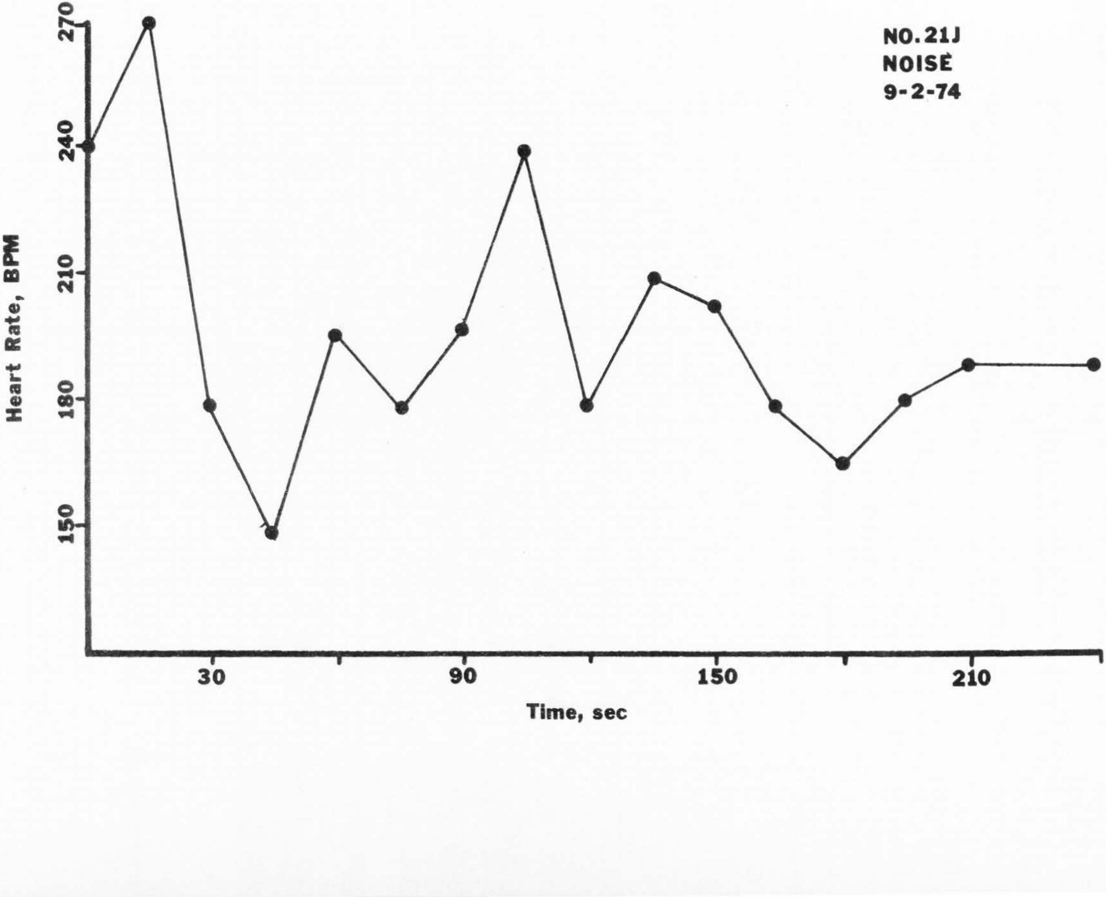
Stress experiments

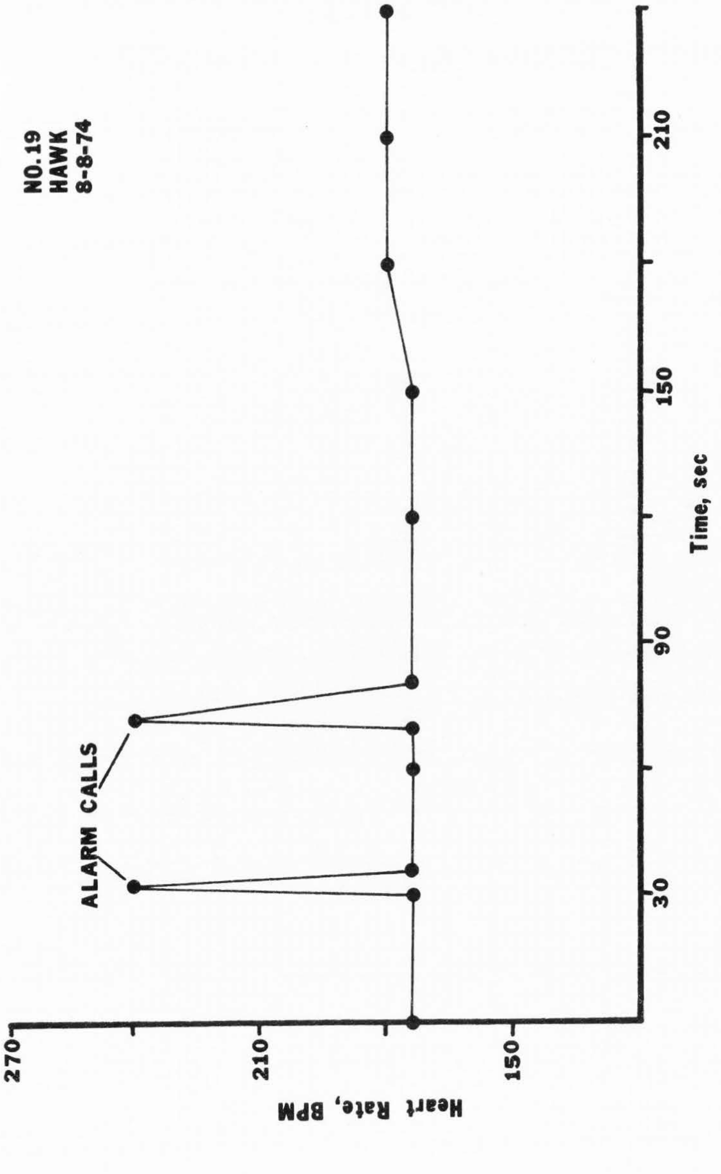
General. From July through September, 1974, 119 stress tests were conducted. Of this number, 22 tests had insufficient data to calculate oxygen consumption and/or heart rate response over time. Therefore, data reported were from 97 stress tests. Patterns of initial response to stimuli were observed in the 97 tests. "Natural" stressors (approximating situations an animal might encounter in the wild, i.e., raptors and mammalian ground predators and conspecifics) tended to decrease in initial heart rate response, 41 of 51 tests decreased. Whereas, "artificial" stressors (such as noise, shock and confinement) tended to have an initial increase in heart rate, 32 of 37 tests increased. Nine tests in "natural" and "artificial" stressors did neither. The response of oxygen consumption to stressors was quite variable and will be reported in later sections. In calculating relationships between heart rate and oxygen consumption of 97 stress tests, 16 had a positive linear relationship ($r > 0.90$), 27 had a positive relationship with a correlation coefficient not statistically significant at 0.05, 9 tended


RMR COMPARISON
NO. 21J AND 23J
NO. 23J
9-16-74
NO. 23J
9-11-74
NO. 21J
9-3-74
NO. 21J
8-30-74
3.0
2.0
1.0
O_2 Consumption, ml/g/hr
100
150
200
250
Heart Rate, BPM

towards a positive linear relationship (only two oxygen consumption levels), 4 had a negative linear relationship statistically significant at 0.05, 17 had a negative relationship which was not statistically significant at 0.05, 6 tended towards a negative relationship, and 18 had no change in oxygen consumption during stress tests even though heart rate sometimes changed. An apparently random occurrence of negative heart rate-oxygen consumption regressions was recorded over all stress tests and all squirrels stressed. In thost stress tests with a negative relationship between heart rate and oxygen consumption, initial heart rate response tended to have a greater increase or decrease (> than 25% change from initial) and occurred in a shorter time period (5 to 10 seconds) than in tests with positive relationships which had less marked changes in initial heart rate response (<30% change from initial) and lasted longer (10 to 30 seconds). In negative heart rate-oxygen consumption relationships oxygen consumption did not change immediately after presentation of the stimulus as did heart rate. Oxygen consumption tended to remain unchanged from 10 to 35 seconds after heart rate changed. After this lapse in time, oxygen consumption responded as heart rate had at stimulus presentation.

After the initial response, heart rate tended to oscillate around an average heart rate for 10 seconds to 12 minutes with the average length of response being 3.4 minutes (Figure 14). The oscillations were more pronounced in some tests than others. Oscillations varied within and between tests with no apparent trend. Another common response of all tests was a rapid increase and decrease in heart rate when an animal gave an alarm call (Figure 15). It was also noted that animals tended to

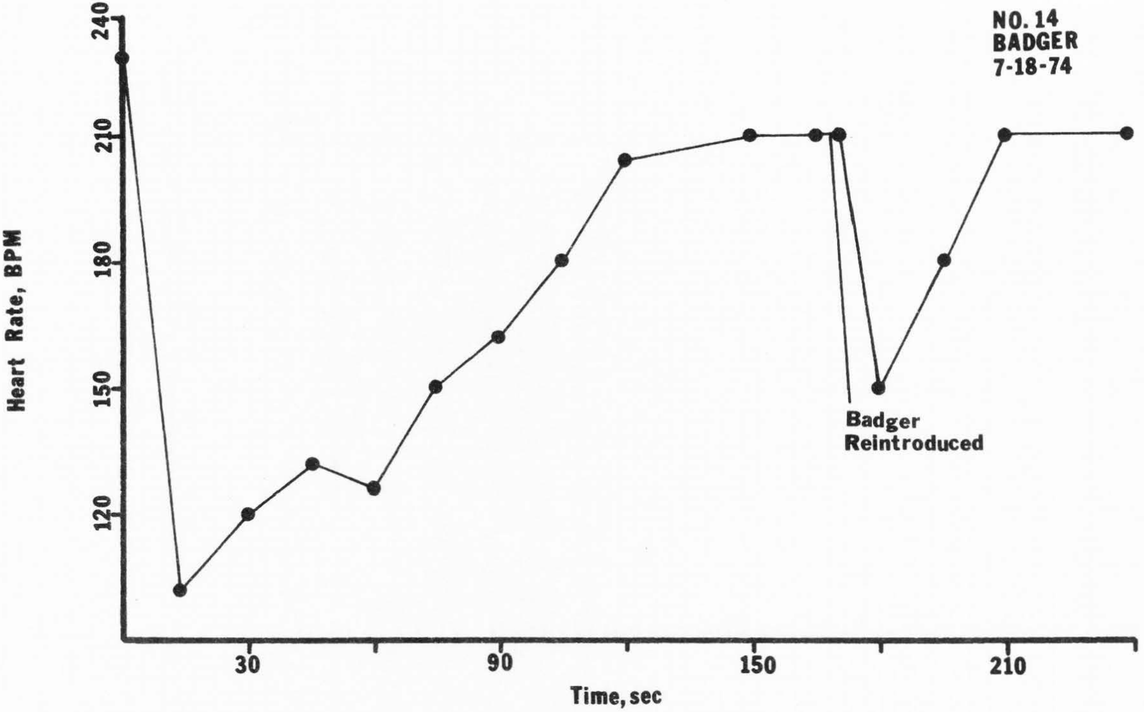

NO. 21J
NOISE
9-2-74
Heart Rate, BPM
270
240
210
180
150
30
90
150
210
Time, sec

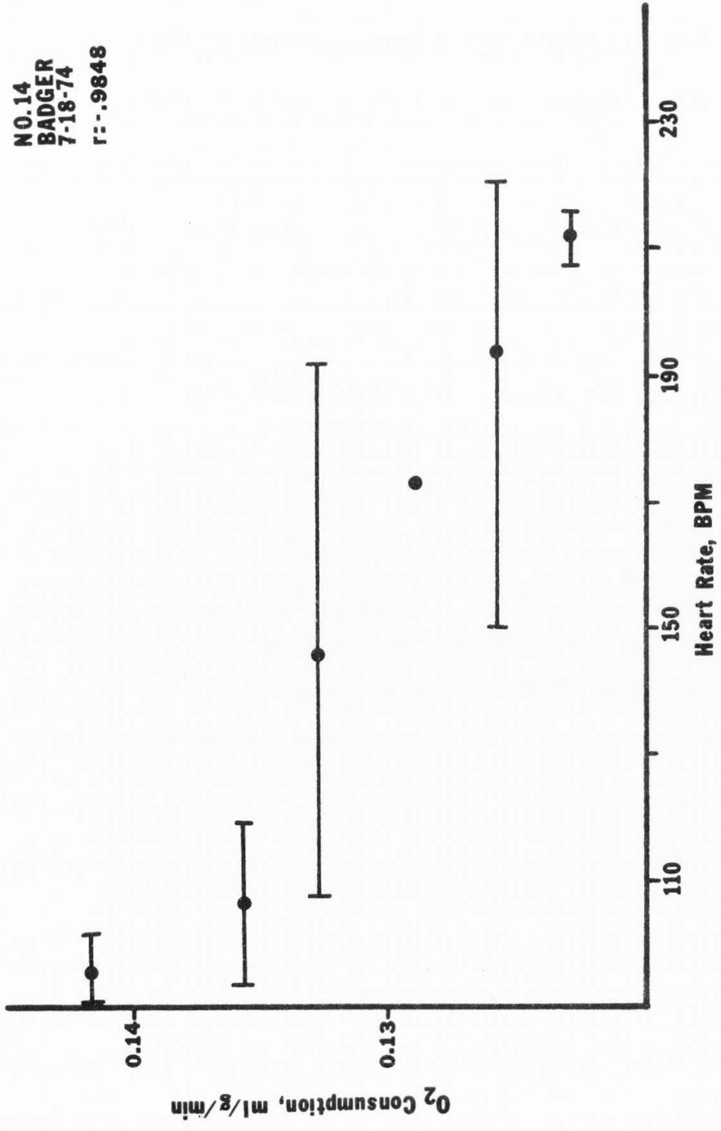

NO.19
HAWK
8-8-74
ALARM CALLS
Heart Rate, BPM
270
210
150
Time, sec
30
90
150
210

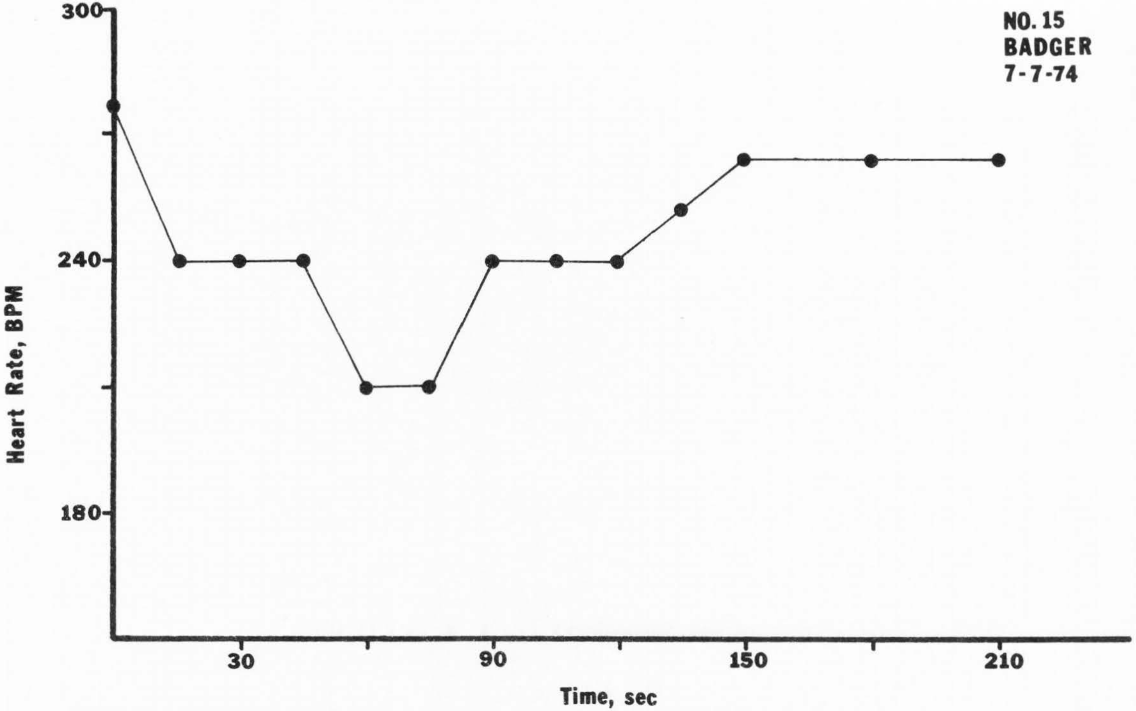
habituate to the stimuli after the first trial (Figure 16). Therefore, each animal was usually stressed on only one occasion. In animals with an initial heart rate below 150 beats per minute (BPM) "natural" stressors usually caused an initial increase in heart rate. While the heart rate of animals with high initial rates (greater than 300 BPM) usually decreased when presented artificial stressors.

Badger. The use of a mounted badger as a "natural" stressor produced two types of heart rate response (Figures 16-19). Table 1 shows that in four of eighteen tests squirrels had an increase in heart rate over pre-stimulus heart rates. In these four tests the pre-stimulus heart rate tended to be low (<168 BPM). Animals with high pre-stimulus heart rates (>144 BPM) had an initial decrease in heart rate response to a stressor. Average heart rate during the response time tended to be lower in animals with low pre-stimulus heart rates and higher in animals with high pre-stimulus heart rates. The total length of response did not appear to be related to pre-stimulus heart rate.

The relationship between heart rate and oxygen consumption was quite variable for this stress test. A positive relationship between heart rate and oxygen consumption was observed in nine of eighteen tests, while a negative relationship was observed in eight tests (Table 1). Little heart rate change and no oxygen consumption change occurred in one test. Three of nine positive linear relationships had correlation coefficients that were statistically significant at 0.05. The remaining six were not statistically significant. Of eight negative linear relationships, two had a correlation coefficient that was statistically significant at 0.05. Four of the negative relationships were not


NO. 14
BADGER
7-18-74
Heart Rate, BPM
240
210
180
150
120
30
90
150
210
Time, sec
Badger
Reintroduced


NO.14
BADGER
7-18-74
r=-.9848
230
190
150
110
Heart Rate, BPM
0.14
0.13
O_2 Consumption, ml/g/min


NO. 15
BADGER
7-7-74
300
240
180
Heart Rate, BPM
30
90
150
210
Time, sec

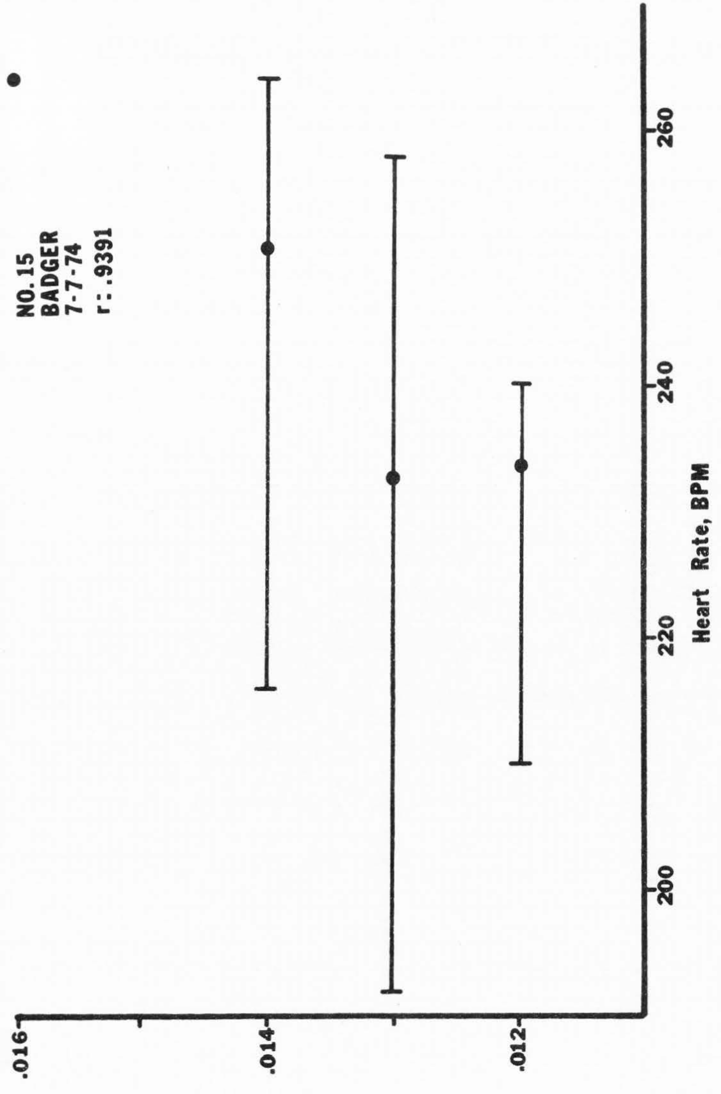

NO.15
BADGER
7-7-74
r: .9391
.016
.014
.012
O$_2$ Consumption, ml/g/min
200
220
240
260
Heart Rate, BPM

Table 1. Heart rate responses of seventeen Uinta ground squirrels to a badger, from July through September, 1974. The correlation coefficients were calculated for linear regression analysis of heart rate versus oxygen consumption

Animal I.D.	Date	Initial heart rate (BPM)	Final heart rate (BPM)	Average heart rate (BPM)	Initial heart rate response (%)	Length of response (Minutes)	Correlation coefficient
15	7-7-74	270	240	241	-11	8	+.939**
14	7-18-74	288	234	190	-61	6	-.985**
4	7-22-74	144	126	118	-38	4	Trend Neg.
5	7-24-75	198	216	183	- 9	4	+.266
10	7-27-74	270	252	247	-16	8	+.962**
8	7-29-74	186	174	179	-10	4	+.762*
17	7-30-74	108	114	113	+11	.5	+.082
18	8-4-75	204	198	176	-52	1	-.028
6	8-6-74	156	162	170	- 4	3	-.196
19	8-8-74	168	174	176	+16	1	+.620
19	8-12-74	228	204	199	+ 8	3	+.220
1	8-13-74	192	120	123	-59	6	-.887*
20J	8-19-74	276	288	290	- 2	6	-.803
26J	8-28-74	224	246	238	- 6	1.5	One point
25J	8-29-74	240	228	215	-25	6	-.832
24J	8-29-74	186	192	183	- 3	2	+.780
21J	9-2-74	138	150	165	+17	8	+.619
22J	9-5-74	250	192	195	-45	4	Trend neg.

*Statistically significant at 0.05
**Statistically significant at 0.001

statistically significant at 0.05 and two relationships tended toward a negative regression (only two different oxygen consumption values were recorded during the tests).

When comparing positive and negative relationships, there appeared to be a trend for all negative relationships to begin with a rapid and large decrease in heart rate as opposed to a slower and less drastic change at the start of positive relationships. Negative relationships were associated with lower average heart rates (185 BPM) and shorter durations of response (4.5 minutes) than positive relationships (207 BPM and 5.7 minutes). No such trends appeared in initial or final heart rates. A seasonal trend in the proportion of positive to negative relationships occurring each month was lacking. Also, all negative relationships between heart rate and oxygen consumption began with an initial decrease in heart rate, whereas positive relationships were observed to have initial increases or decreases in heart rate.

Owl and hawk. Use of a mounted owl for the first 10 stress tests in this series provided inconclusive results possibly due to the fact that an owl is not a normal predator of ground squirrels. Table 2 shows that only two of ten tests had three or more oxygen consumption values. Therefore, calculation of linear regression line for heart rate versus oxygen consumption was not possible in eight of the ten tests. In the two tests in which three or more oxygen consumption levels were measured the negative correlations were not statistically significant at 0.05. A rapid initial decrease in heart rate occurred in these two tests (Figure 20). The response of animal number 17 was contrary to that which was normally observed. The response was an initial increase in

Table 2. Heart rate response of sixteen Uinta ground squirrels to a hawk and an owl, from July through September, 1974. The correlation coefficients were calculated for linear regression analysis of heart rate versus oxygen consumption

Animal I.D.	Date	Initial heart rate (BPM)	Final heart rate (BPM)	Average heart rate (BPM)	Initial heart rate response (%)	length of response (Minutes)	Correlation coefficient
				Owl			
15	7-7-74	276	276	245	-13	4.5	One point
15	7-7-74	252	252	197	-45	1.5	One point
14	7-18-74	192	210	167	-66	10	-.545
4	7-22-74	138	138	134	-35	2	-.564
5	7-23-74	180	180	180	00	0	No change
8	7-29-74	180	180	179	-17	5	Trend pos.
17	7-30-74	114	114	118	+37	.5	Trend neg.
18	8-5-74	192	192	172	-31	1.5	One point
19	8-8-74	180	168	167	- 8	1	Trend neg.
6	8-6-74	150	150	134	-52	.5	One point
				Hawk			
6	8-6-74	135	150	131	-31	1.5	One point
19	8-8-74	174	180	181	- 7	00	+.975**
19	8-12-74	210	186	209	+15	.5	+.995**
1	8-13-74	120	114	109	-19	1.5	One point
8	8-13-74	312	300	274	-30	1.5	One point
20J	8-19-74	300	300	295	-31	3	-.988*
26J	8-28-74	232	216	229	+25	1.5	+.896
25J	8-29-74	210	216	211	+ 9	1	+.114
24J	8-29-74	156	156	175	-30	2.5	Trend pos.
21J	9-2-74	168	180	161	0	3	Trend pos.
22J	9-5-74	186	210	202	-11	3	One point

*Statistically significant at 0.05

**Statistically significant at 0.001

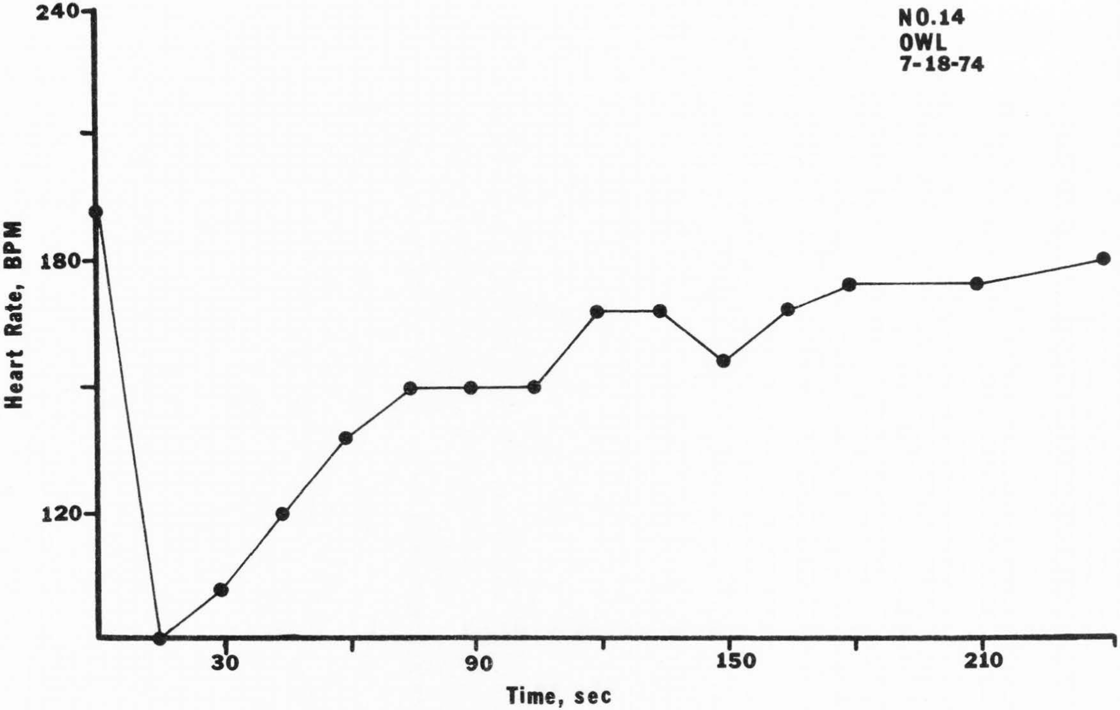


Figure 20. Heart rate response of a Uinta ground squirrel to an owl, under laboratory conditions in 1974.

heart rate with a negative correlation between heart rate and oxygen consumption. This was a test with just two oxygen consumption recordings and the correlation could only be stated as a trend. If the relationship with two points for oxygen consumption are considered, the trends in average heart rate and response duration were similar to those in the badger tests. That is, average heart rate was lower (147 BPM) and length of response shorter (3.35 minutes) for negative relationships than for positive relationships (179 BPM and 5 minutes).

When a cardboard silhouette of a hawk was presented to test animals, the heart rate-oxygen consumption relationships for six of eleven squirrels could not be calculated, due to an insufficient number of oxygen consumption values. Two of six values did have a two-point trend. Those relationships which were negative or tended toward a negative correlation had rapid initial decreases in heart rate. Positive relationships had either initial increases or slow decreases (Table 2). Four of the five positive relationships between heart rate and oxygen consumption began with increases in heart rate. The trend toward negative relationships with large initial decreases in heart rate was apparent from these data with the exception of a two-point positive trend in squirrel 24J. Figure 21 illustrates a response pattern that begins with an initial increase of 15% to 180 BPM followed by a plateau of heart rate for 5 seconds and then a subsequent increase over 25 seconds to 228 BPM or 30% above initial heart rate. In four of eleven tests, animals responded to presentation of the hawk model with an alarm call. Figure 15 shows the response of heart rate after an alarm call. Heart rate-oxygen consumption relationships are positive and usually linear during the period

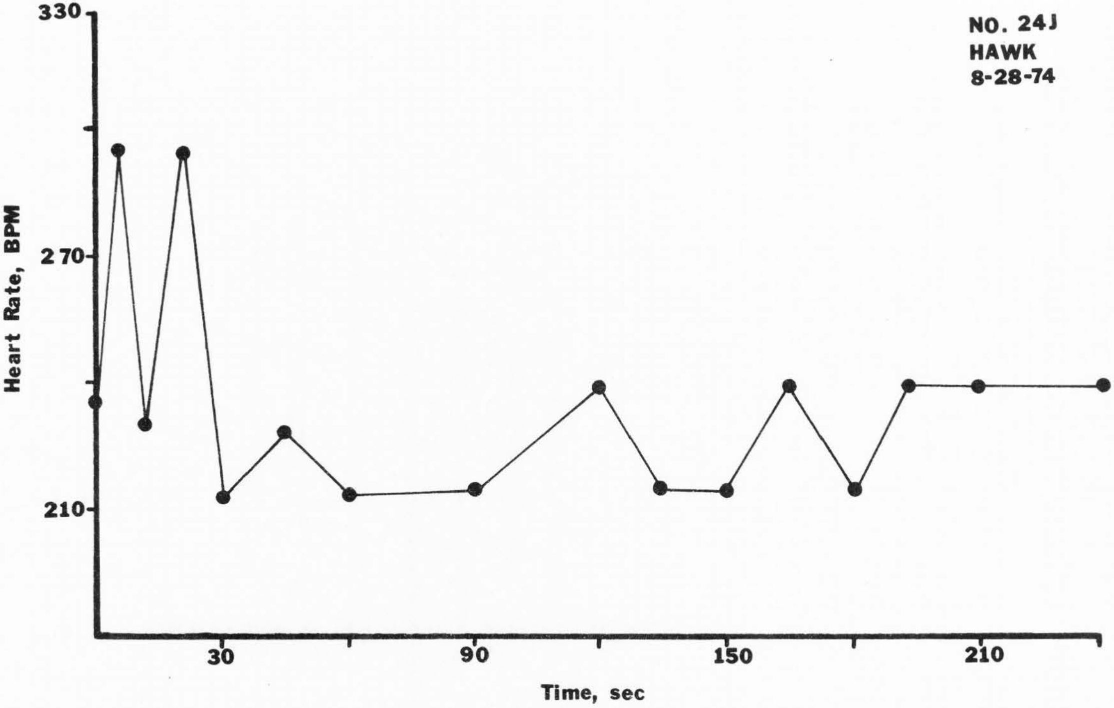


Figure 21. Heart rate response of a Uinta ground squirrel to a hawk, under laboratory conditions in 1974.

of the call. Both increases and decreases in initial heart rate occurred in squirrels whose heart rate-oxygen consumption regression was positive and linear or tended to vary in this way. In those individuals with increasing heart rates, pre-stimulus heart rates (with the exception of number 24J) were all above 200 BPM. Pre-stimulus heart rates below 200 BPM were followed by decreasing heart rates except those of squirrels number 8 and number 20J.

Conspecific. As in the previous three "natural stressors, the majority of heart rates decreased initially. In this tests, 12 of 14 initial heart rate responses decreased. Figure 22 is a representation of the typical response. The sex of the stressor squirrel appeared to have no effect on the heart rate-oxygen consumption relationship of squirrels stressed. Of 14 tests, four had one oxygen consumption value and two had two values (Table 3). As in the owl and hawk stress tests, it appeared that the squirrel was not responding to the stimulus as in the badger tests. This was also apparent in average lengths of response (2 minutes) in most tests with a positive heart rate-oxygen consumption relationship. In those squirrels with negative responses, initial decreases in heart rate tended to be smaller (-11%) compared to observed negative responses with other stressors. In one interesting test with a conspecific, the heart rate of squirrel number 19 did not change initially, but was followed by a series of rapid increases and decreases in heart rate over short periods of time as the animal gave an alarm call (Figure 15). When plotting heart rate versus oxygen consumption, the relationship was linear and positive.

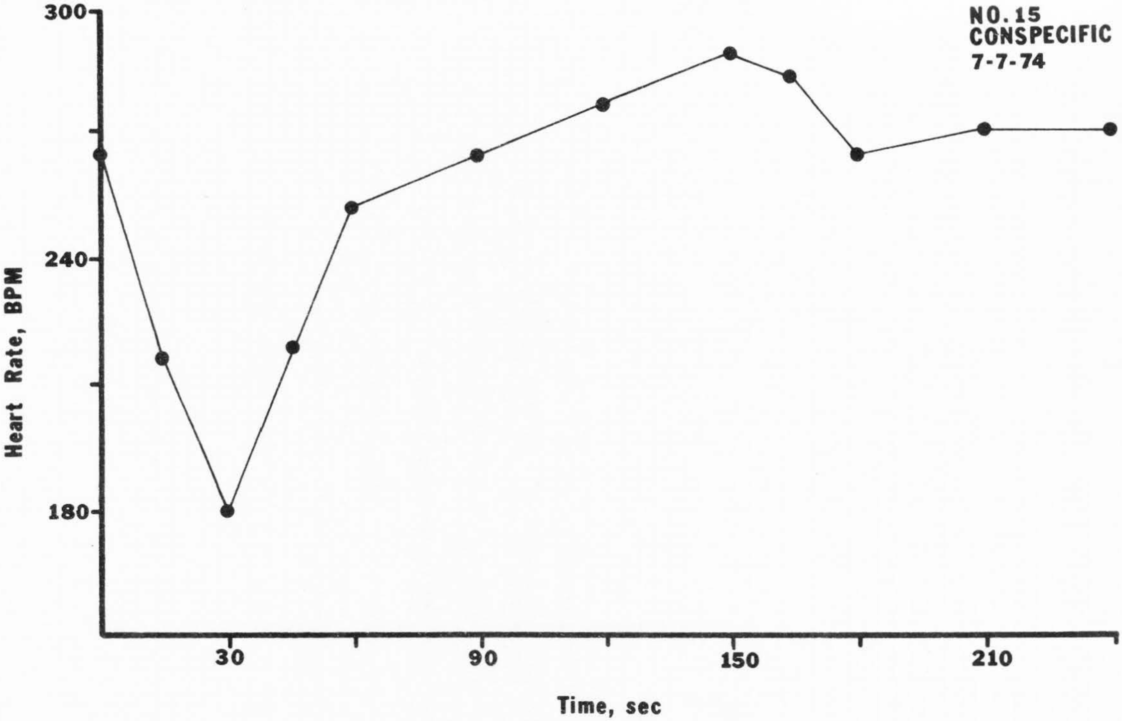


Figure 22. Heart rate response of a Uinta ground squirrel to a conspecific, under laboratory conditions in 1974.

Table 3. Heart rate response of thirteen Uinta ground squirrels to a conspecific, from July through September, 1974. The correlation coefficients were calculated for linear regression analysis of heart rate versus oxygen consumption

Animal I.D.	Date	Initial heart rate (BPM)	Final heart rate (BPM)	Average heart rate (BPM)	Initial heart rate response (%)	Length of response (Minutes)	Correlation coefficient
15	7-7-74	264	270	245	-32	3	+.996**
14	7-18-74	204	234	178	-56	3.5	+.168
4	7-22-74	120	120	121	- 5	0	-.211
5	7-23-74	198	198	178	-21	1.5	One point
8	7-29-74	180	180	183	- 7	8	-.155
17	7-30-74	132	114	118	-14	.1	One point
18	8-5-74	204	204	179	-17	2	+.557
6	8-6-74	140	156	190	+29	4	+.902
19	8-12-74	192	192	193	- 6	0	+.950*
1	8-13-74	132	138	133	-21	1	Trend pos.
8	8-13-74	276	288	262	-53	1.5	One point
26J	8-26-74	227	247	244	+18	1.5	One point
25J	8-29-74	276	228	207	-41	1	Trend pos.
21J	9-2-74	162	210	196	-11	8	-.484

*Statistically significant at 0.05

**Statistically significant at 0.001

Shock. Current through the animal in shock stress tests varied from 1.0 to 2.0 mA. The current depended on which axis of the squirrel's body served as the resistance, i.e., whether the circuit was completed between the animals front legs, hind legs or through the long axis of the body, from front to hind legs. The stimulus was applied at a frequency of 10 pulses per second for a 10 second period. In most cases the stimulus shock caused interference in heart rate recordings. Therefore, heart rate recording was usually absent for the first 10 seconds of the stimulus period. In five of fourteen tests conducted, neither heart rate nor oxygen consumption changed (Table 4). In these cases the squirrels may not have been shocked due to breaks in the shock grid from squirrel movement. Dried feces also accumulated on the shock grid system prior to the period of actual testing. In three of fifteen tests, two oxygen consumption values were observed which tended toward a positive relationship between heart rate and oxygen consumption. In two of fifteen tests, heart rate and oxygen consumption were negatively correlated but the coefficient was not statistically significant at 0.05. Squirrels with an initial decrease in heart rate had negative heart rate-oxygen consumption relationships, while squirrels with either initial increases or decreases in heart rate had positive heart rate-oxygen consumption relationships. The average length of response for negative relationships was 2.1 minutes and 6.3 minutes for positive relationships. The magnitude of the initial responses were similar for positive and negative relationships. The response time did not appear to vary between the two relationships. Squirrels with a positive relationship between heart rate and oxygen consumption tended to have larger fluctuations in

Table 4. Heart rate response of thirteen Uinta ground squirrels to shock, from July through September, 1974. The correlation coefficients were calculated for linear regression analysis of heart rate versus oxygen consumption

Animal I.D.	Date	Initial heart rate (BPM)	Final heart rate (BPM)	Average heart rate (BPM)	Initial heart rate response (%)	Length of response (Minutes)	Correlation coefficient
14	7-18-74	186	174	165	0	0	One point
4	7-22-74	120	120	146	+50	5	+.212
5	7-23-74	180	180	227	+67	6	+.964*
10	7-27-74	240	264	262	+15	8	+.880**
17	7-30-74	126	126	126	-29	7	+.990*
18	8-5-74	198	198	193	+ 6	.5	One point
6	8-6-74	144	144	148	-15	.5	-.938
19	8-8-74	180	192	197	No response	0	One point
19	8-12-74		No response				
8	8-13-74	300	270	288	-14	4	-.500
26J	8-26-74	222	222	221	+28	1	Trend pos.
24J	8-29-74		No response				
21J	9-2-74	174	210	223	+55	1	Trend pos.
22J	9-5-74	210	216	211	- 9	2	Trend pos.

*Statistically significant at 0.05
**Statistically significant at 0.001

heart rate after termination of the stimulus and continuing for 30 seconds to one or two minutes (Figure 23).

Noise. As in shock stress tests, initial heart rate increased in response to noise in 14 of 15 tests (Table 5). Figure 24 represents a typical heart rate response of squirrels to noise. The only animal that did not increase heart rate in response to noise was number 8 which had an initial heart rate of 300 BPM, well above most other initial heart rates. There appears to be no distinguishing characteristic between positive and negative heart rate-oxygen consumption relationships other than duration of response. The duration of response of squirrels with negative relationships was 6 minutes, compared to 2.5 minutes for squirrels with positive relationships. There was no trend in initial or average heart rates or magnitude of initial response. Occurrence of negative relationships was observed in two juvenile female ground squirrels, numbers 21J and 22J in early September.

Confinement. Confinement stress tests were implemented to determine the response of a squirrel's heart rate and oxygen consumption to an extreme stimulus. The typical response of a squirrel to confinement is shown in Figures 25 and 26. Of 13 tests conducted, five squirrels had a linear relationship between heart rate and oxygen consumption, one relationship being negative and four relationships being positive. In the remaining eight squirrels, the relationships were not linear (correlation coefficient not statistically significant at 0.05) with six relationships being positive and two relationships being negative (Table 6). All animals responded to the stimulus with an initial increase in heart rate. Squirrels with negative relationships between heart rate

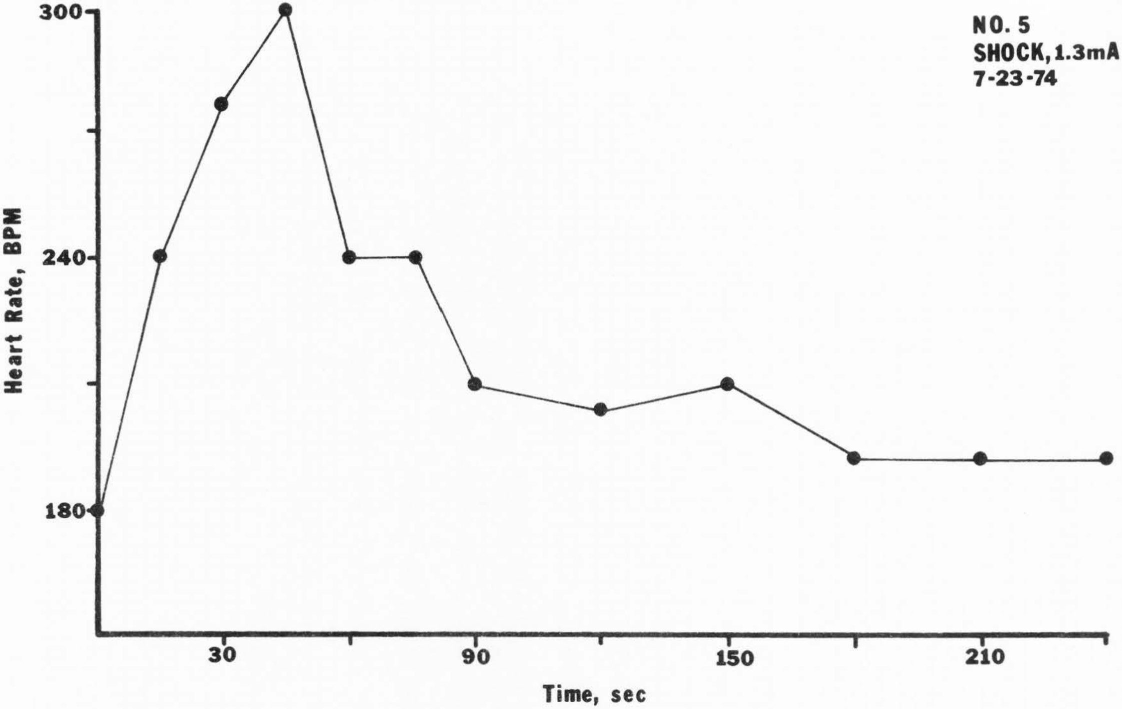


Figure 23. Heart rate response of a Uinta ground squirrel to a 1.3 mA shock for 10 seconds, under laboratory conditions in 1974.

Table 5. Heart rate response of thirteen Uinta ground squirrels to noise, from July through September, 1974. The correlation coefficients were calculated for linear regression analysis of heart rate versus oxygen consumption

Animal I.D.	Date	Initial heart rate (BPM)	Final heart rate (BPM)	Average heart rate (BPM)	Initial heart rate response (%)	Length of response (Minutes)	Correlation coefficient
5	7-23-74	234	180	194	+15	.5	+.904
17	7-30-74	120	120	134	+50	5	+.861
17	8-1-74	120	132	135	+55	9	+.904
18	8-5-74	198	198	188	+21	3	+.451
6	8-6-74	144	158	172	+75	2	+.863
19	8-8-74	198	186	191	+36	1.5	+.538
19	8-12-74	192	192	203	+20	4	+.982*
1	8-13-74	120	150	156	+100	1.3	+.766
8	8-13-74	300	300	302	-12	1.5	+.992**
20J	8-19-74	288	294	300	+15	.5	One point
26J	8-26-74	264	252	253	-13	4	+.780
25J	8-29-74	228	216	211	+ 5	.6	+.999**
24J	8-29-74	162	162	180	+48	4	+.315
21J	9-2-74	240	180	200	+19	10	-.791
22J	9-5-74	210	186	207	+34	2	-.979*

*Statistically significant at 0.05
**Statistically significant at 0.001

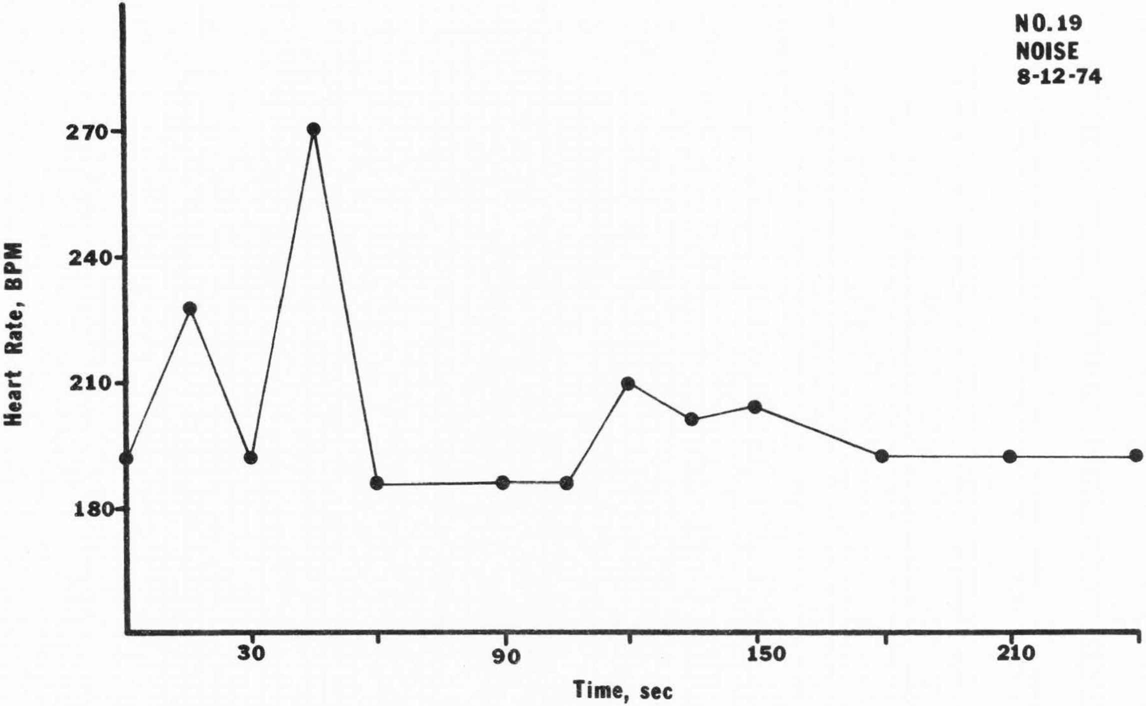


Figure 24. Heart rate response of a Uinta ground squirrel to noise, under laboratory conditions in 1974.

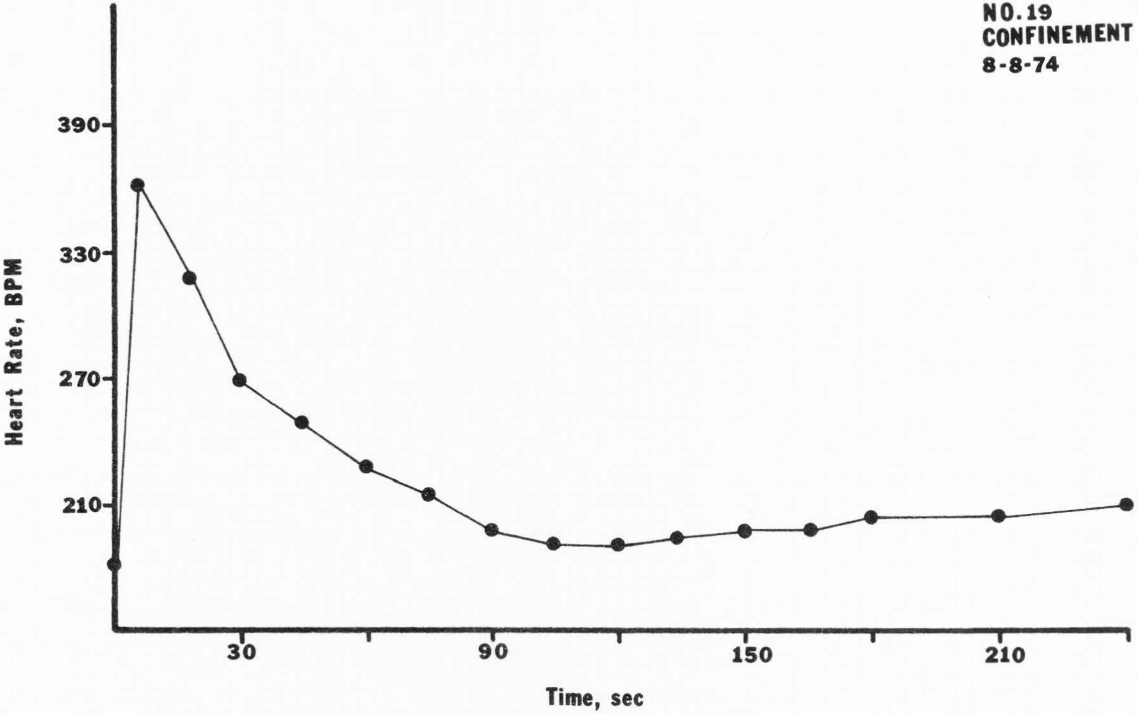


Figure 25. Heart rate response of a Uinta ground squirrel to confinement, under laboratory conditions in 1974.

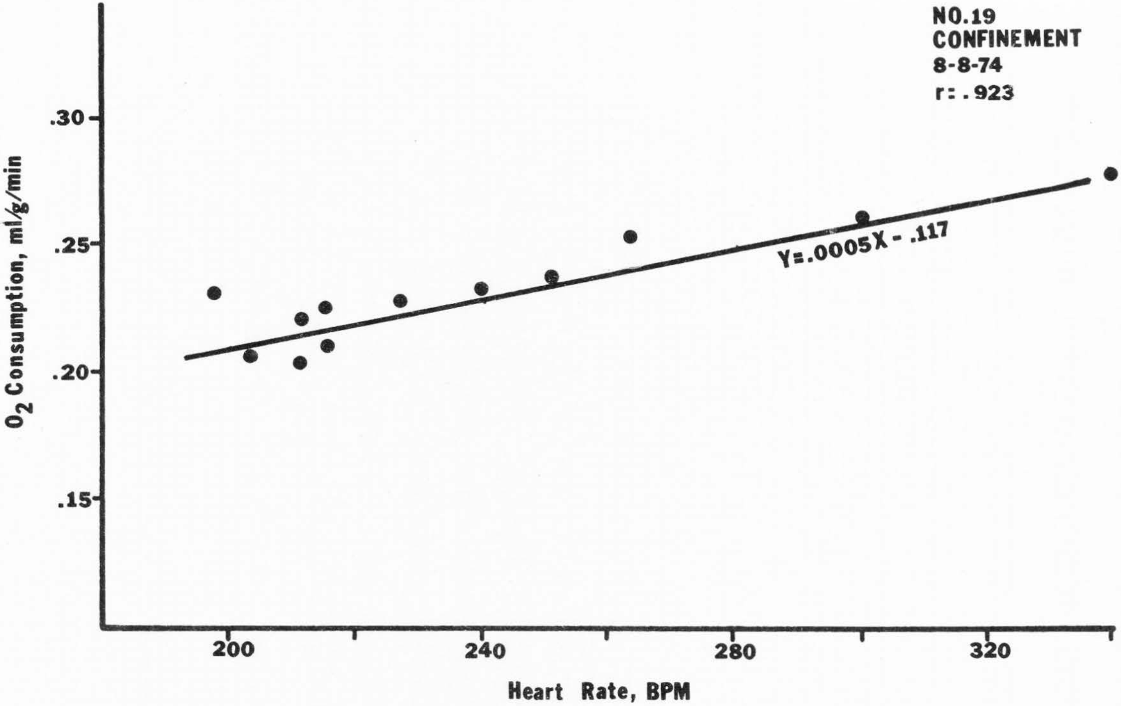


Figure 26. Heart rate-oxygen consumption relationship of a Uinta ground squirrel in response to confinement, under laboratory conditions in 1974.

Table 6. Heart rate response of thirteen Uinta ground squirrels to confinement, from August through September, 1974. The correlation coefficients were calculated for linear regression analysis of heart rate versus oxygen consumption

Animal I.D.	Date	Initial heart rate (BPM)	Final heart rate (BPM)	Average heart rate (BPM)	Initial heart rate response (%)	Length of response (Minutes)	Correlation coefficient
17	8-1-74	131	180	210	+186	4	+.162
18	8-5-74	204	240	291	+97	1.5	-.922**
6	8-6-74	168	228	295	+132	2.2	+.198
19	8-8-74	168	216	235	+114	5	+.923**
19	8-12-74	192	216	289	+88	1.5	+.911**
1	8-13-74	138	240	193	+130	5	+.531
8	8-13-74	252	258	252	+61	4	-.189
20J	8-19-74	270	312	315	-24	1	-.057
26J	8-26-74	228	280	335	+82	12	+.665
25J	8-29-74	218	240	234	+27	2	+.692*
24J	8-29-74	174	252	303	+114	7	+.365
21J	9-2-74	168	234	217	+114	5	+.838**
22J	9-5-74	192	192	174	+41	2.5	+.566

*Statistically significant at 0.05
**Statistically significant at 0.001

and oxygen consumption tended to have a lower average initial response (+60%) when compared to the average initial response of positive relationships (+103%). Squirrels with positive relationships between heart rate and oxygen consumption tended to have pre-stimulus heart rates below 200 BPM (except numbers 26J, 228 BPM and 25J, 218 BPM). Squirrels having negative relationships between heart rate and oxygen consumption had initial heart rates above 204 BPM. The average length of response for negative relationships was also shorter (2.5 minutes) than for positive relationships (4.5 minutes).

Semi free-living experiments

Observations of the change in heart rate concomitant with various behaviors were made on 10 Uinta ground squirrels from June through September, 1974, in an enclosure simulating natural habitat of the squirrels. Heart rate and behavior were monitored for 93 hours on 10 squirrels. Activity was condensed into four categories: feeding, encounters, other above ground activity and in the burrow. Feeding behavior was defined as any activity which was associated with feeding (e.g., periods of complete immobilization when not in an encounter situation; short, rapid running; and upright posture). Encounters were defined as those activities in which an animal was in direct physical contact with another squirrel or when there were any types of threats. The category of other above ground activities included grooming, drinking, sunning, etc. Squirrels spent a great deal of time in the burrow systems during monitoring periods. Heart rate was monitored during these times because the squirrels were often active in the burrows. Table 7 illustrates the percentage of time each squirrel spent in the four categories of activity.

Table 7. Percentage of time semi free-living Uinta ground squirrels spent in various activities from June through September, 1974.

Animal I.D.	Date	Total hours Observed	Percent of time spent				Average heart rate	
			Feeding	Encounter	In Burrow	Other	In Burrow (BPM)	Out of Burrow (BPM)
14	6-15-74	4	30	--	69	1	210	247
14	6-16-74	6	55	1	40	4	246	254
14	6-17-74	5	46	1	50	3	240	275
15	7-4-74	7	65	1	29	5	174	206
15	7-5-74	7	57	2	35	6	180	234
13	7-12-74	5	48	6	42	4	229	271
10	7-25-74	5	43	2	52	3	216	233
10	7-27-74	4	56	1	41	2	216	287
17	7-31-74	7	59	2	34	5	180	185
17	8-1-74	6	49	1	44	6	174	172
18	8-6-74	5	33	---	64	3	252	252
18	8-8-74	Dead						
19	8-11-74	8	62	3	31	4	216	255
21J	9-2-74	5	34	1	61	4	249	315
22J	9-8-74	6	51	1	42	6	155	200
23J	9-19-74	7	42	4	45	9	216	257
23J	9-20-74	6	39	3	50	8	216	267
Total		93	Ave = 48	2	45.4	4.6	Ave[a] 215	254

[a] Without #17

Squirrels averaged 48% of their time in feeding activities; 2% in encounters; 5% in other activities; and 45% in burrows. Of the time spent in above ground activities 87.3% was spent in feeding, 3.6% in encounters and 9.1% in other activities. Average heart rate in the burrow was 213 BPM and average heart rate out of the burrow was 246 BPM.

The behavior of squirrels in the enclosure appeared to be similar to that of free-living Uinta ground squirrels which were observed in 1971. There was more actual contact (i.e., grooming each other and touching one another and more encroachment upon individual distance in semi free-living squirrels. In fact, the squirrels behaviorally and physiologically (heart rate remained the same) appeared to ignore one another for the most part. For this reason, there may have been fewer encounters than in free-living squirrels. The physical environment appeared not to affect behavior of the squirrels. Ambient and burrow temperatures averaged 4°C warmer in the enclosure than at the field site where the animals were trapped. Burrow temperatures in the enclosure were 2-4°C warmer than at the field site depending on the burrow measured and its exposure to the sun.

Heart rate response of semi free-living ground squirrels was of two general types: either an increase or a decrease in response to stimuli. The heart rate then remained at the newly attained level for varying lengths of time. Figures 27 and 28 illustrate the types of response a squirrel may show. Figure 27 shows heart rate response of an animal at the onset of an encounter over food. Figure 28 indicates length of time over which changes occurred. The second response is a decrease in heart rate over a 40 second period. Figure 27 also

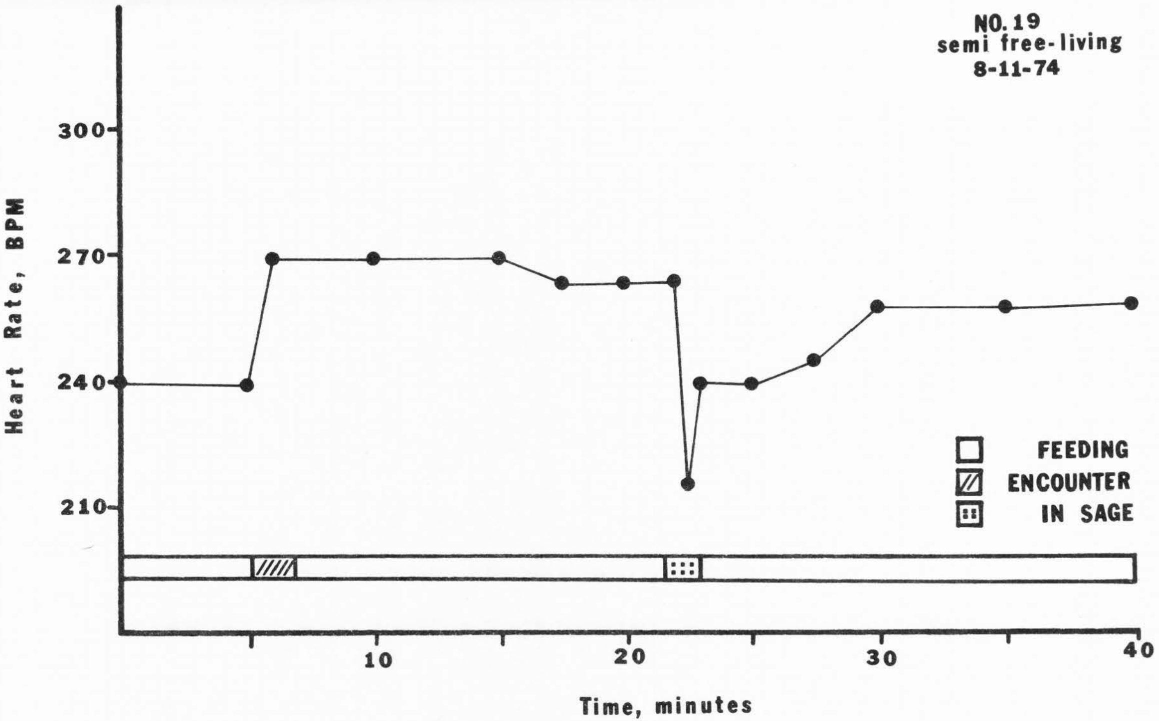


Figure 27. Heart rate of a semi free-living Uinta ground squirrel monitored over a forty minute period in August, 1974.

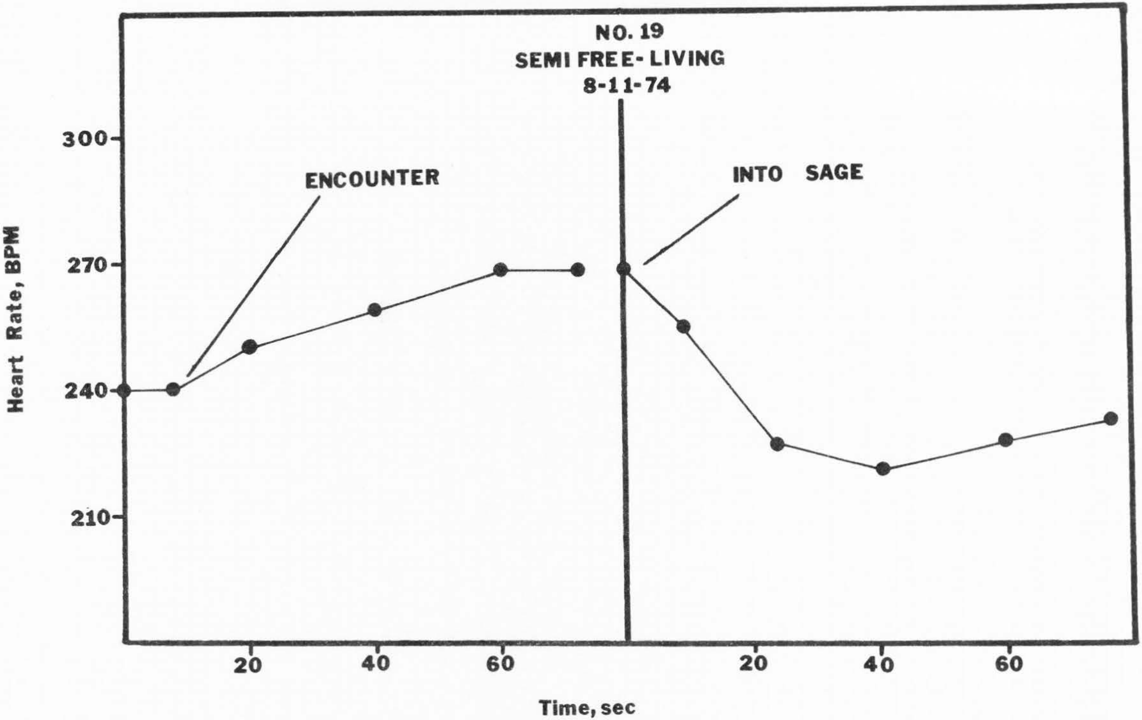


Figure 28. Typical heart rate responses of a semi free-living Uinta ground squirrel to two environmental stimuli.

illustrates that the major portion of a ground squirrel's above ground activity is spent in feeding. During these periods of feeding, heart rate fluctuates only a few beats per minute.

DISCUSSION

Resting metabolic rate-heart rate measurements

The relationship between heart rate and oxygen consumption of resting Uinta ground squirrels under laboratory conditions with changes in air temperature was found to be linear as in previous study on Uinta ground squirrels (Johnson, 1973). A linear relationship could be expected when an animal is tested under resting conditions with no physical exertion. Johnson and Gessaman (1973) reported several studies of birds and mammals in which both heart rate and metabolism increased linearly with decreasing ambient temperatures. They inferred from these studies that metabolism is a linear function of heart rate during changes in ambient temperature.

The percentage difference between the average oxygen consumption (13.6 l. 0_2/animal/day) of seven squirrels monitored by Johnson in 1971 and that (14.3 l. 0_2/animal/day) of eight squirrels that I monitored when their heart rate was 250 BPM was 5%. From these data, resting metabolic rates measured in the artificial burrow and in paint cans as used by Johnson are similar. There may be three explanations for this: 1) animals in paint cans or other small metabolism chambers may not be stressed as was thought by Gebczynski (1966); 2) the artificial burrow used in this study may be stressing squirrels to the same degree as paint can metabolism chambers; or 3) bringing squirrels from the field into the laboratory may be a stressor. I feel the first explanation is probably correct, metabolism chambers do not stress the squirrel, because the range of heart rates monitored on ground squirrels in the chamber was similar to the range of heart rates observed in free-living ground squirrels monitored in 1972.

Changes of heart rate-oxygen consumption relationships with time have been recorded in three separate studies on small rodents. Morhardt and Morhardt (1971) reported variability of heart rate versus oxygen consumption between individuals of the same species and body weight as well as within a single individual on different days. The slopes and shapes of the regressions did not vary greatly, but did affect the variability of the overall correlation. They also reported an accuracy of predicting oxygen consumption from heart rate of ±25% to ±150%. Johnson (1973) found the slopes of heart rate-oxygen consumption regressions differed significantly over a five-day period. The standard deviations of two regressions did not overlap indicating the regressions were two different relationships. Lund (1974) observed that the slopes and elevations of heart rate-oxygen consumption regressions changed very little over periods of a few days. In addition he reported that the relationships did not change significantly over periods of weeks or months, however variability between regression lines over longer measurement periods decreased the accuracy of predicting absolute values of oxygen consumption from the regression.

Relationships found in this study between heart rate and oxygen consumption of Uinta ground squirrels agree with the studies of the Morhardt's and Lund in that, over long periods of measurements, weeks or months, slopes and elevations of regression lines do not change significantly. Although slopes and elevations were not significantly different in any of these studies, there were variations between individual regression lines that affected oxygen consumption prediction from heart rate. The variability in predicting oxygen consumption from average regression equations in this study was ±10% to ±80% for eight individuals as compared to ±25% to ±150% variability observed by the Morhardts. The heart rate-oxygen consumption regression was less stable over periods of a few days in my study than in the studies of Lund (1974). The slope of the heart rate-oxygen consumption relationship which I measured and which were reported by the Morhardts did not change significantly during these short time periods, but the elevation of the relationships did change in several cases within a few days. The variability of regression lines over a few days in this study was ±15%. The possible reason for the greater variability in Morhardt's and my average regressions as compared to Lund's is that some of Lund's were measured over a one or two day period. If this relationship between heart rate and oxygen consumption is a dynamic one, the longer period between measurements in my study may be causing greater variability than was observed in Lund's study. The results of Johnson (1973) on Uinta ground squirrels indicate that the prediction of oxygen consumption may not even be as accurate as I have shown. He reported the slope and elevation of the heart rate-oxygen consumption relationship of two squirrels measured initially and five days later was significantly different. However, his studies were conducted on individuals in January when the squirrels are normally in hibernation and this may have caused a physiological imbalance in the animal. The results of the studies of Johnson (1973), Morhardt and Morhardt (1971), and Lund (1974) and the present study indicate that the use of the heart rate method for predicting resting oxygen consumption may be a good method. However, the regression of heart rate-oxygen consumption appears to be a dynamic relationship which may even change daily. One should measure the heart rate-oxygen consumption relationship immediately before and after the period of monitoring the squirrel in the field.

Stress experiments

Heart rate response of Uinta ground squirrels to various stressors employed in this study had trends similar to heart rate responses of other animals in previous studies. The typical response of a Uinta ground squirrel to a predator was an initial decrease in heart rate. Green (1969) observed a similar response in Peking ducks when presented with a goosehawk model moved overhead. Mancia, Baccelli and Zanchetti (1972) observed a similar initial decrease in heart rate of cats when a threatening cat was presented to a test cat. However, when a barking dog was presented, heart rate of the test cat initially increased. Heart rate response of individuals to conspecifics and predators was similar, a decrease in initial heart rate. Ruff (1971) observed that heart rate increased initially in most social encounters of free-living Uinta ground squirrels. He also observed initial decreases in heart rate when squirrels were in a calling-bout. This may have been the response observed in this study because animals were calling during the conspecifics studies, more so then in other stress tests. The decrease in heart rate in response to conspecifics in this study as opposed to a general increase in heart rate in squirrels studied by Ruff may have been due to the absence of olfactory cues to the test animals which were in an airtight chamber. Furthermore, test animils were non-pregnant and non-lactating females, whereas, Ruff studied pregnant and lactating females which are extremely territorial during this time. A study of pregnant and/or lactating females may show a similar increase in initial heart rate to conspecifics.

The other type of general initial heart rate response observed in stress experiments was an increased heart rate in response to noise, shock and confinement. A similar heart rate response was observed in pre- and post-weaning rats (Chalmers and Levine, 1974). They reported that 21 days post-parturition rats had increased initial heart rates in response to a shock of 2mA for .1 second duration. The typical response to noise was an initial increase in heart rate as has been reported by Bond (1943) in dogs and cats, Keefe (1970) in humans, Morhardt and Morhardt (1971) in six species of rodents, and Lund (1974) in black-tailed prairie dogs.

The general response of heart rate to various stressors can be broadly grouped into two categories: initial increase in heart rate in response to "artificial stressors" (i.e., noise, shock and confinement) or initial decrease in heart rate in response to "natural stressors" (i.e., predators and conspecifics). Increases or decreases in initial heart rate in response to stimuli have been observed by Boas (1932), Galin and Lacey (1972), Jackson (1974), Lacey and Lacey (1958), Obrist et al. (1970), Roessler, Collins and Burch (1969) and Smith and Strawbridge (1969). Increases and decreases have been defined by Sokolov (1963) as a defensive reflex in which the quality of the stimulus is the determining factor. An initial increase in heart rate response is the usual defensive reflex response. A decrease in initial heart rate should occur in what Sokolov terms the orienting reflex.

In the orienting reflex, the animal is increasing the sensitivity of its sensory organs to facilitate environmental input. Lacey et al. (1963) also defined these responses in a similar manner. That is, stimuli which evoke attention to the environment induce cardiac deceleration, while those evoking rejection of the environment induce cardiac acceleration. Lacey and Lacey (1974) theorize that

> attention to the external environment, particularly in awaiting signal stimuli, produced a cardiac decrease which is part of a cardiovascular depressor response whose resultant afferent feedback stimuli, primarily from baroreceptors, might serve the function of improving both the organism receptivity to afferent stimulation and organisms readiness to make effective responses to such stimuli.

Obrist et al. (1970) theorizes that the initial heart rate decrease may not be involved in an afferent mechanism but as a peripheral manifestation of central processes. That is, initial heart rate decrease may be due to decreased metabolic demands associated with decreased motor activities. Elliott (1972, 1974) argues that there is little direct evidence to support the cardiovascular feedback theory of Lacey. He suggests that decrease in heart rate response to stimuli may be a part of a general quieting response involving a variety of somatic and visceral events while the animal awaits the stimulus. He is saying that the change in heart rate is an effect rather than a cause of a response to a stimulus.

The heart rate response trends observed in my study appear to be more readily explained by the theory of Lacey and Lacey (1974). That is, in the natural stressors, where there is a lower discriminability of the external environment, initial heart rate tends to decrease, while, in artificial stressors, high stimulus intensity, initial heart rate tends to increase. These responses do not agree with the hypothesis of Obrist et al. (1970) and to some extent Elliott (1972) because the responses were quite rapid and of relatively short duration. If the responses were a result of decreased metabolic demands due to a decreased motor activity, the response should be at a slower rate because of the buffering ability of the cardiovascular system.

Initial heart rate response to a stimulus may not always decrease with stimuli evoking an orienting reflex or increase with stimuli evoking a defensive reflex (Elliott, 1974). This variation in response was observed in my study and could be due to the emotional state of the squirrel which is difficult to ascertain. A few, but not all deviations from expected heart rate responses in my study may be explained by the Law of Initial Values (LIV) defined by Wilder in 1931 and again discussed by him in 1962. The LIV states the magnitude of a physiological response to a stimulus is related to the prestimulus level according to the following: "given a standard dose of stimulus and a standard period of measurement, the response, defined as the change from the initial level, will tend to be smaller when the initial value is higher" for function raising stimuli. For function inhibiting stimuli, the higher the initial value, the greater the decrease in the variable examined. According to LIV, if the initial levels are extremely high and a stimulus normally causing an increase is applied, the heart rate will decrease rather than increase. According to Hord, Johnson and Lubin (1964) this would occur because a high heart rate already has a high level of tonic activitiy and a further increase would be held in check or a decrease may occur due to parasympathetic activity. The LIV did not hold in all cases in my study. Hord, Johnson and Lubin (1964) demonstrated that the LIV was operating only in those cases where there is a rapid and direct negative feedback on the output of the organ system. Hutt and Hutt (1970) also observed that less intense stimuli did not elicit responses expected by the LIV. Heart rate responses which deviated from normal responses in my study may have been due to absence of negative feedback from vagal innervation or a low stimulus intensity.

Another general trend in heart rate over the stress experiments was a fluctuation of the heart rate around some average value during the period between presentation of stimuli and return of heart rate to prestimulus levels. Bond (1943) observed similar fluctuations in the heart rate of dogs and cats in response to a loud noise. He observed a rapid increase in heart rate in response to noise and a subsequent decrease within ten or more seconds. Heart rate would then oscillate around an average value for two to three minutes and occasionally as long as seven minutes. The magnitude of the fluctuations varied for different animals tested. This same pattern was noted in my study. Initial response to a stimulus, whether increasing or decreasing heart rate, peaked between 5 and 45 seconds with oscillations lasting from 90 seconds to 12 minutes. Bond (1943), Donald and Shepherd (1963), Obrist, Wood. and Presez-Reyes (1965), Hamlin et al. (1972), Scher et al. (1972) and Obrist et al. (1974) reported that initial increases or decreases in heart rate are linked to decreased or increased vagal efferent activity respectively. Obrist, Wood and Presez-Reyes (1965) and Obrist et al. (1974) noted sympathetic effects on the heart are normally minimal but may be evoked by intense stress. Bond (1943) and Scher et al. (1972) observed sympathetic responses were slower than vagal responses by 8-12 seconds in dogs, lending support to the theory that initial changes in heart rate are due to vagal efferent responses. Bond (1943) theorized that "the undulations that often take place after 60 seconds are interpreted as being due to overswinging of the pressor receptors."

Regressions of oxygen consumption on heart rate were quite variable during stress experiments. There was a trend toward a linear relationship between heart rate and oxygen consumption in those tests in which heart rate reached its highest or lowest value in 20 seconds or more after stimulus presentation. Twenty percent of the statistically significant linear relationships had a negative correlation. In those tests where the initial heart rate response reached the high or low value within 5 to 10 seconds the relationship tended to be negative (60% of the time), i.e., as heart rate decreased oxygen consumption remained constant. In those tests with decreasing initial heart rate, the oxygen consumption would remain constant from 5 to 20 seconds and then follow the response of heart rate by a lag time of 5 to 20 seconds. This response may be a peculiarity to hibernators. Lyman (1958) observed the heart rate of woodchucks entering hibernation declined prior to a decrease in oxygen consumption by less than 5 minutes. Heart rate and respiratory rate changes have also been monitored on animals entering hibernation or torpor. Landau (1956) and Landau and Dawe (1958) reported that respiratory rate preceded heart rate changes when 13-lined ground squirrels entered hibernation. Morhardt (1970) reported breathing rate and heart rate fell rapidly during daily torpor in white-footed mice. However, it was not apparent which rate responded first.

He did report that decreases in heart rate and breathing rate followed a linear trend. The results of Lyman (1958) are not contradicted if breathing rate changes precede changes in heart rate. Leitner and Nelson (1957), Taylor and Sale (1964), Bartholomew, Leitner and Nelson (1964), and Bartholomew and Nelson (1971) showed oxygen consumption was not linearly related to respiratory rate during changing ambient temperatures in several species of bats and hyrax. At high ambient temperatures, oxygen consumption changes lagged behind respiratory rate changes. If oxygen consumption and respiratory rate behave similarly under stressful conditions, this would explain differences in the results of Landau (1956) and Lyman (1958). Therefore, if Uinta ground squirrels have a response similar to the woodchuck, the lag in oxygen consumption after heart rate changes might be expected. Respiratory rate may decrease prior to the change in oxygen consumption. It would be necessary to monitor respiratory rate, oxygen consumption and heart rate simultaneously under stress conditions to determine if this pattern of physiological change is occurring.

A lag in oxygen consumption change with changing heart rate may also be caused by a slower transport of blood. Blood may take approximately 10 seconds to pass from the metabolizing organs to the pulmonary capillaries. Another possible cause of lag in oxygen consumption changes may be a response reported by Astrand and Rodahl (1970). They reported that if a subject is moved from a horizontal position to a feet-down position, cardiac output falls due to venous pooling. Heart rate will increase when this occurs. As the muscle pump is activated and propels blood to the heart, heart rate may decrease as stroke volume increases. In the vertical position, oxygen consumption remains constant indicating the A-V_{O_2} difference is increased. If at the onset of a stimulus venous pooling occurs in squirrels, this may explain the lag in oxygen consumption. This is probably not occurring because there were no initial increases in heart rate followed by decreases in heart rate in any tests with a lag in oxygen consumption. However, in these explanations one fact is puzzling, that is, the lag in oxygen consumption occurs in some squirrels and tests and not in others with no apparent pattern. To resolve this problem, research on the physiological parameters which may be changing (i.e., stroke volume and A-V_{O_2} difference) will be necessary.

Semi free-living experiments

I observed that semi free-living Uinta ground squirrels spend a large portion of the day in their burrows. Ruff (1971) reported similar observations on free-living Uinta ground squirrels and Lund (1974) on free-living black-tailed prairie dogs. The activities of the squirrels above ground included feeding, encountering conspecifics, grooming, drinking, digging as well as other activities. Of these activities, feeding comprised the major portion of above ground activity. Lund (1974) reported a similar observation in black-tailed prairie dogs. During periods of feeding, heart rate remained fairly constant indicating that one should be able to predict reasonable oxygen consumption values from heart rate during these periods. Similarly, Owen (1969) found that heart rate of semi free-living blue-winged teal (*Anas discors*) did not change much during feeding.

Responses of heart rate to changing activities of semi free-living ground squirrels were similar to some heart rate patterns observed in stress experiments. The heart rate of semi free-living ground squirrels either increased or decreased to a new level of heart rate within 20 seconds or more after the onset of the stimulus. This is similar to responses observed in stress tests in which heart rate-oxygen consumption relationships tended to be linear with a positive slope. However, this is only a trend, many regression coefficients were not significant. Therefore, heart rate is undoubtedly not a good predicator of oxygen consumption during these periods of rapid transition in heart rate.

On the other hand, prediction of oxygen consumption from heart rate over daily periods should be more accurate. Bradfield, Huntzicker and Fruehan (1969) hypothesized that average heart rate over periods of hours would be a better predictor of oxygen consumption than heart rates for short activities when an average energy expenditure value is necessary.

Although the Morhardt's (1971) reported it was "not feasible to predict absolute levels of VO_2 from heart rate unless technical improvements can reduce the variability," I feel that present data on heart rate-oxygen consumption relationships of Uinta ground squirrels indicate this method would be a reasonable predictor of free-living energy expenditures when averaged over hourly or daily periods. Data from three different analysis support this contention. First, heart rate was monitored on five free-living Uinta ground squirrels in 1971 and 1972 (Gessaman, Oldfield and Johnson, 1975). Heart rate and oxygen consumption were measured in the laboratory and metabolism of the free-living animals was computed from laboratory heart rate-oxygen consumption relationships. Metabolism computed from heart rate of free-living ground squirrels averaged 2.59 times greater than standard metabolism computed from the equation of Kleiber (1961). This factor is similar to the values used by Brody (1945), 3 times standard metabolic rate, and that used by Golley (1960), 2 times standard metabolic rate to account for the cost of daily activity. Second, Johnson (1973) monitored heart rate and carbon dioxide production (Haldane method) of a Uinta ground squirrel in a metabolism chamber for two days. Metabolism predicted from heart rate was compared with measured carbon dioxide values. Metabolism calculated from carbon dioxide values was 10% greater for each day than metabolism predicted from heart rate. Third, metabolism predicted from heart rate of free-living Uinta ground squirrels in burrows was 18.7% greater than metabolism predicted from estimated burrow temperature from data of Gessaman, Oldfield and Johnson (1975). The latter calculation was based on a burrow temperature of 27°C which is assumed to be an upper limit of burrow temperature. Soil temperature at burrow depth is 15°C in late June (Oldfield, 1973). Metabolism predicted from heart rate is 20.0% less than metabolism predicted from a burrow temperature of 15°C. If one assumes a burrow temperature at an intermediate value, 20°C, metabolism predicted from heart rate is 6% less than metabolism predicted from burrow temperature. A measured value of burrow temperature is needed before a definite percent difference is known. However, a burrow temperature of 20°C seems to be realistic because summer burrows of Uinta ground squirrels have little if any nest material to increase insulation for the squirrel in the burrow. Therefore, it seems that for non-pregnant, non-lactating female Uinta ground squirrels the heart rate method is a reasonable predictor of 24 hour metabolism.

CONCLUSION

The relationship between heart rate and oxygen consumption is stable, positive and linear over periods of less than one day for non-pregnant and non-lactating female Uinta ground squirrels. However, regressions of oxygen consumption on heart rate change over several days for the same squirrel. The regression is also different between individual Uinta ground squirrels. To use laboratory measured heart rate-oxygen consumption regressions to predict daily oxygen consumption of free-living squirrels over several days it is necessary to determine whether the regression has changed during the monitoring period. Heart rate-oxygen consumption regressions should be measured before and after each individual is monitored under field conditions. If the regression does change, an average of the two regression lines could be used for predicting oxygen consumption from heart rate.

The stress test used in this study generated two types of heart rate response to stimuli, an increase or decrease in initial heart rate response. Relationships between heart rate and oxygen consumption tended to be linear. However, a great many relationships were not statistically significant. Some stress tests produced a negative linear relationship between heart rate and oxygen consumption. That is, oxygen consumption remained constant as heart rate decreased. The lag in oxygen consumption with decreasing heart rate which has been observed in the woodchuck entering hibernation, may be occurring in stressed ground squirrels.

Heart rate changes generated by stress tests were also observed in semi free-living Uinta ground squirrels. These would suggest that heart rate is not a reliable predictor of oxygen consumption of semi free-living squirrels when it is changing rapidly. However heart rate remains relatively stable during feeding which is the major above ground activity of both semi free-living and free-living squirrels. Therefore, heart rate should be a reasonable predictor of daily oxygen consumption of free-living squirrels. While the animal is in the burrow, heart rate remains at a fairly constant level, again indicating that heart rate should be a reliable predictor of oxygen consumption over time periods greater than one hour. Previous studies on this same population of Uinta ground squirrels under free-living conditions indicate that heart rate predicts reasonable values of oxygen consumption over daily periods.

It appears that heart rate is a reasonable predictor of free-living oxygen consumption of non-pregnant, non-lactating female Uinta ground squirrels for hourly or daily periods if heart rate-oxygen consumption relationships are calculated before and after free-living experiments. This method would not be applicable to studies in which minute by minute values of oxygen consumption are required, particularly during activities when heart rate is changing rapidly.

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